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THE SENSORY LINE SYSTEM AND THE CANAL BONES IN THE HEAD OF SOME OSTARIOPHYSI

BY

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LIC. PHIL.

(From the Zootomical Institute, University of Stockholm.)

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I. INTRODUCTION.

The lateral line system of the bone fishes has been subjected to a number of more or less comprehensive investigations. However, attention has, on the

whole, been directed only to the canal system of body and head. The pit-line system has not been studied to the same extent. Extensive lists of literature on the forementioned subjects have been provided by MANIGK (1933) and STENSIÖ (1947).

As far as fishes belonging to the sub-order *Ostariophysi* are concerned, investigations regarding the lateral line system are scarce and, partly, very incomplete. Best known is the family of the *Silurids,* through investigations carried out by POLLARD (1892), COLLINGE (1895), HERRICK (1899, 1900, 1901), ALLIS (1904) and FRIEDRICH-FREKSA (1930). POLLARD and COLLINGE have discussed the canals in adult specimens only. ALLIS has also, in some degree, examined the pit-lines, while HERRICK has performed thorough analyses of the lateral line and nervous system, especially in *Menidia* and *Ameiurus.* Finally, FRIEDRICH-FREKSA has described *Plotosus* with its ampullae of Lorenzini.

In spite of its rich variety in species and individuals, the family of the Cyprinids has not been made the subject of any particularly minute studies. In 1904 ALLIS gave an account of the canal system in *Carassius* and *Moxostoma,* mentioning that, as to the canals, *Tinca* conforms to the last-mentioned fish. In his work on the cranium of the Cyprinids, SAGEMEHL, in 1891, also deals, to some extent, with the canals of the head. Further, *Tinca* was discussed by ANDRES (1899). Unfortunately, his paper has not been available in Sweden. A detailed account of the fully developed lateral line system in *Phoxinus* was submitted by MANIGK (1933). He has also given an extensive description of the nervous system. Finally, DEVILLERS (1944 c and 1947), studied the canal system in the adult *Leuciscus.* In this respect ALLIS (1904) examined the *Characinids* and in 1884, SAGEMEHL made some passing references to the canal system of these fishes. As far as I am aware, the family of the *Cobitids* has not been investigated in this respect.

In their works on the development of the lateral line system in fishes, published in recent years, HOLMGREN (1942) and STENSIÖ (1947) have particularly stressed the lack of data regarding the origin and development of this system in Teleosts. This explains why these authors have not been in a position to deal with the fishes concerned, except in a comparatively summary manner.

In the present paper the purpose has been partly to supply, as far as possible, embryologic data, partly to describe the lateral line system in some species of the suborder *Ostariophysi,* a group of fishes that, as stated above, has so far been but scantily studied. With this object in view, I have examined, chiefly, a number of Cyprinids and some Cobitids. The author is well conscious of the fact that it might have been desirable to examine a larger number of species and families. However, in this work the attention has been concentrated on a few different representatives in order to obtain a conception of the lateral line pattern and its origin in this group of fishes.

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At the same time, the origin and development of the canal bones have been studied. Also in this respect our knowledge regarding the Teleosts is incomplete. Only a few species have been investigated in detail, in the first place *Esox* (PEHRSON 1944 a) and various Salmonids (SCHLEIP 1904, PEHRSON 1944 a, and DEVILLERS 1944 a, b and 1947). With a view to certain comparisons, DEVILLERS has also discussed the formation and development of the canal bones in *Leuciscus* (1947). For the rest, as far as the *Ostariophysi* are concerned, no representative has been carefully studied, at all events not with regard to the earliest origin of the bones. In this connection mention may, however, be made of KINDRED's paper of 1919, on the development of the cranium in *Ameiurus*.

As far as available material has permitted, the development of the bones has, in the present investigation, been studied from their first formation up to adult state. Whenever developmental stages are missing, only the conditions in the adult fish have been described. The attention has been particularly directed to the interrelation between the lamellar and latero-sensory components of the canal bones and the genesis of these two components.

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This work has been carried out at the Zootomical Institute of Stockholm's Högskola, and I am happy to use this opportunity to express my deeply felt gratitude to Professor Emeritus NILS HOLMGREN, late Chief of the Institute, and to Professor TORSTEN PEHRSON, his successor, for their kind and untiring interest in my work and for their advice with regard both to practical and theoretical problems. I also wish to record my obligation to Professor ERIK STENSIÖ for helpful suggestions and discussions. I am indebted to Professor HIALMAR RENDAHL for valuable material of *Plotosus*.

II. MATERIAL AND METHODS.

For the present investigation the following section series have been at my disposal:

Abramis blicca: 40 mm (2 specimens).
Alburnus alburnus: 7.9, 9.4, 10.5, 14, 15.8, 18, 20, 22, 42 mm.
Cobitis taenia: 38, 70 mm (2 spec.).
Leuciscus rutilus: 114h, 116h, 119h (3 spec.), 141h, 191h, 195h, 390h, 333h, 5 mm (5 spec.), 5.2, 5.4 (3 spec.), 5.5 (2 spec.), 5.8, 6.0 (2 spec.), 6.3 (3 spec.), 6.6, 6.8, 7.0, 7.4 (2 spec.), 7.5 (3 spec.), 7.6, 7.8, 8.0, 8.1, 8.5, 9.0, 9.5, 10, 11, 12, 14, 16, 18, 20, 22, 24, 26, 44 mm.
Nemachilus barbatula: 3.0, 3.4, 4.0, 4.3, 4.5, 5.5, 6.0, 6.6, 7.8, 8.1, 9.0, 9.3, 12, 14, 17, 18, 20, 21, 23, 26, 33, 47, 70 mm.
Phoxinus phoxinus: 6.0, 6.2, 6.3, 7.1, 7.3, 7.5 (2 spec.), 7.6, 7.7, 7.8, 7.9,

8.0, 8.1, 8.3, 8.5, 8.6, 8.9, 9.4, 10, 11.5, 11.7, 12, 12.7, 16, 17.5, 23, 27, 35, 47, 50, 60 mm (2 spec.).

Plotosus anguillaris: 43 mm.

Tinca tinca: 46 mm.

For the purpose of certain comparisons I have, in addition, been granted access to the extensive collection of section series of bony fish, available at the Zootomical Institute. (For a catalogue of this collection, see HOLMGREN 1943, page 4).

As regards fixation, BOUIN's solution has been chiefly used for major specimens, SMITH's solution (1912) for minor ones. This latter fluid has proved exceedingly useful and far superior to BOUIN's. For the staining of nerves, fixation 2 acc. BODIAN has been employed. The section series have been stained with Azan-Mallory, acc. HEIDENHEIN's modification. Nerve staining has been performed according to the method recommended by BODIAN (ROMEIS 1943). For smaller specimens, a section thickness of 6 μ proved most suitable, for major specimens 10—15 μ.

All reconstructions have been carried out according to the graphic method. They have been based on photographic negatives of the sections.

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III. THE LATERAL LINE SYSTEM.

1. THE EARLIEST FORMATION OF THE LATERAL LINE SYSTEM.

As stated in the introductory remarks, the fully developed lateral line system has been discussed in a great many works. Investigations concerning the formation and development of this system are, on the other hand, comparatively few and partly incomplete. In Teleosts, this system has not been studied from its first formation till its full development. Among investigations regarding its earliest formation, WILSON (1891), who examined *Serranus atrarius* should be mentioned. In a later work the same author, together with MATTOCKS (1897), described an early stage of *Salmo*. CLAPP (1898), gave an account of the formation and development in *Batrachus*. In addition, mention should be made of BEARD (1884, 1885), and LANDACRE (1910), who examined the origin of the cranial ganglia in *Ameiurus* and, in this connection, also discussed the earliest formation of the lateral line system.

Unlike most vertebrates, the central nervous system of Teleosts is not formed by two neural ledges, but through a thickening of the medial part of the neural plate which afterwards, wedgewise, projects downwards. In this way, the dorsal side of the future central nervous system will lie approximately in a line with the indifferent ectoblast, rising but slightly above it. This indifferent ectoblast will merge into the primordium of the central nervous system,

without any marked delimitation, contrary to the conditions, for instance, in the Amphibians, where the delimitation is clearly outlined. On each side of the neural primordium in *Leuciscus* and *Salmo*, a pronounced epithelial thickening is distinguishable, parallel with the neural primordium, constituting a transition zone between the latter and the rest of the ectoblast, viz. "the lateral mass" (LANDACRE). At an early stage two cellular layers are clearly discernible. This has been observed by a great many authors. The external layer of the epidermis, the "Deckschicht" (SALENSKY 1881), the "couche supérieur, lame enveloppante" (HENNEGUY 1888), is composed of an exceedingly thin cellular stratum, the flattened cells of which lie sparsely. Below this stratum a thicker one is to be found, the "Grundschicht" (SALENSKY), the "lame nerveuse" (HENNEGUY). In this layer the cellular nuclei lie at a right angle to the body surface. The cells of the forementioned ectodermal thickening are easily distinguishable from the cells in the surrounding epidermis because of their size and cylindrical shape. Towards the middle of the ectodermal thickening this basic layer forms an epithelium divided in several strata which passes into the medullary primordium without any distinct boundary. At a slightly later stage, when the medullary cord has become detached from the rest of the ectoblast, the lateral epithelial thickening can easily be distinguished from the medullary primordium. Thus, at this stage, a marked and well delimited placode exists, the socalled dorsolateral placode. The interpretation of the origin of this placode differs from one author to another. In the opinion of GOETTE (1878), the lateral parts of this, as yet partly undifferentiated, medullary plate forms a socalled sensory plate. GORONOWITSCH (1885) and others denied this view, stating that this plate is derived from ectoderm already severed from the medullary cord. A similar view was expressed by BEARD (1888), who considered that it arises from a thickening of the epidermis, laterally to the neural plate, and is always separated from it. In principle, WILSON and MATTOCKS (1897) share GOETTE's opinion. They maintain that, in the course of the development of the medullary plate, a comparatively thick part of the ectodermis is left close on each side of it. "This streak is", they state, "the lateral sensory Anlage, and it is to be noticed that it is not *produced* as a thickening, but is *left over* during thinning out of the shield." LANDACRE (1910) ascertained in young stages of *Ameiurus* that "the neural crest and dorsolateral placodes are not differentiated from each other at first and appear as a large lateral thickening, lying on either side of the neural plate". "This", he says, "I have designated as the lateral mass. It doubtless contains regions comparable to the neural crest and certainly to the dorsolateral placodes of other authors." In *Salmo* and *Leuciscus*, the position agrees in detail to LANDACRE's fig. A—D, page 326. Thus, the dorsolateral placode, probably, consists of the same material from which the central nervous system is initiated.

This thickening extends along the entire head of the fish, being composed of

high cylindrical cells, partly multi-stratal. In the portions immediately in front of and behind the future auditory vesicle, the placode is relatively narrow and high. Further in front it becomes broader and correspondingly thinner, the material having extended over a wider surface.

For a short period of the development, at least in *Salmo*, two neuromasts may form in the placode in front of the eye, one just behind the eye and another in front of the auditory vesicle. After an exceedingly short time these organs disappear, like the rest of the placode, as well as the placode behind the auditory vesicle. The material in it will be spread over a larger surface of the head, part of it apparently also being changed into mesenchyma. Within the same area, in front of and behind the auditory vesicle, placodes, from which the lateral system will definitively arise, are again formed. Whether the primary placode has any direct connection with the lateralis placodes is difficult to determine. On this point opinions differ. Thus, *Serranus* (WILSON 1889) is different in several respects. The lateral line system, the auditory vesicle, the nasal placode and the lens arise from a common primordium, viz. a long "sensory furrow" at the side of the head. This furrow is divided into three parts, the first of which initiates the lateralis system of the head, the middle one the auditory vesicle and the hindmost the lateral line of the body. The anterior part which is, originally, invaginated, as the auditory vesicle, though its lumen will afterwards disappear, offers the appearance of a large sense organ, i.e. a branchial sense organ from which a sensory cord of cells runs forwards. As regards the future fate of it, WILSON makes the following statement: "The anterior sensory tract is at the time of hatching very short, and just what becomes of it, I do not know." Further, he states that the preauditory placode disappears, while the corresponding placode behind the auditory vesicle grows backwards, initiating the lateral line of the body. After the disappearance of these formations in front of the eye neuromasts are later formed in the same area.

In *Ameiurus* LANDACRE (1910) has ascertained that parts of the lateral mass differentiated into an auditory vesicle and pre- and postauditory placodes, while the rest of the lateral mass more or less breaks down into mesenchyma from which, inter alia, parts of the acustico-lateralis ganglia form. The preauditory placode changes into mesectoderm, and does not initiate the lateral line system, there being a few hours' interval between the breaking-down of the placode and the formation of the first neuromasts. The same applies to the placode behind the auditory vesicle which also breaks down without giving rise to any lateralis organs. Still, a vago-lateralis ganglion is formed from cells proliferated from this placode. The lateralis organs arise by means of a gradual differentiation of the deeper layers in the epidermis, sometimes alone, sometimes two together from a common primordium, being, as far as their origin is concerned, totally separate from the placode.

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As to the derivation of the lateral line system in *Batrachus*, CLAPP (1898) states: "Immediately after the closure of the auditory pits, thickenings of the lower layer of the ectoderm are observed on each side of the head in the preauditory region. From this thickened area two cords extend, one above and another below the eye. These cords are the rudiments of the supraorbital and infraorbital lines of the sense organs." Evidently, CLAPP has not analysed earlier stages. Her examination begins when the definitive lateral placodes already are forming. BECKWITH (1907), who has studied the earlier formation of the lateralis system in *Amia*, arrived at the conclusion that it does not grow out from the auditory vesicle but is formed as local differentiations in the epidermis, in which the neuromasts will later appear.

In this respect the Amphibians seem to differ from fishes. Also in the Amphibians there is "a common primordium which has the form of a continuous longitudinal thickening of the ectoderm that skirts the anterior and lateral sides of the primitive neural plate" (KNOUFF 1935). The ear with its ganglia, as well as the ganglia and sense organs in the lateral system, develop from the acustico-lateral thickening. The preauditory placode proximally differentiates into the lateralis VII ganglia, while distally forming the general primordium of the supraorbital and infraorbital lateral line placodes and, probably, the hyomandibular lateral line placode. The postauditory placode forms the corresponding parts of the lateral line system behind the auditory vesicle.

To sum up, from the above short survey it is evident that a well developed dorsolateral placode forms in the Teleosts, at an early stage, from the same material as the central nervous system. From this sensory placode, the auditory vesicle will, inter alia, originate, while in the part immediately in front of it either a big sense organ (*Serranus*) or a pair of small organs (*Salmo*) or no organs at all (*Ameiurus*) will appear. In all these examined fishes the organs and the entire placode totally disappear. It is dissolved into mesenchyma and will partly initiate lateralis ganglia. A short time after the disappearance of the placode, secondary placodes arise in the same area, which in due course originate the lateral line system. Whether these two placode generations have anything in common is difficult to say. As stated above, this is denied by certain authors. In *Salmo*, the placode is, from the beginning, pronounced and well delimited but, in the course of the development, it will become more and more diffuse, while the material extends over large parts of the head. In all probability, this placode does not only give rise to the lateralis ganglia but also constitutes the initial material of other parts of the lateral line system, i.e. the definitive lateralis placodes.

2. THE LATERAL LINE SYSTEM IN *LEUCISCUS RUTILUS* L.

No account is available of the lateral line system in its entirety. DEVILLERS (1944 c and 1947) describes the canal system in this fish, while only briefly referring to the pit-line system.

A. The origin and development of the pit-line system.

The first primordium of a definite lateral line system in this fish appears when it is about 110 hours old (in water about 10° C). Thus, in a specimen, 116 hours old (fig. 1), two well developed placodes appear, situated immediately in front of the auditory vesicle (*a.v.*), though completely independent of it. These two placodes are connected caudally, but separated rostrally. The upper placode (*so.p.*), i.e. the bigger one, constitutes the first primordium of the posterior part of the supraorbital line, while the lower one (*o.p.*), which is only half its size, forms the primordium of the intertemporal organs innervated by the otic nerve. Likewise, in *Batrachus*, CLAPP (1898) described the first primordia of the lateral line system in the preauditory region, in the shape of a thickened epithelial area. The placodes are formed in the deeper parts of the epithelium in the basal layer, while the epithelial cover, which, to begin with, remains wholly intact outside the placodes, takes no part in their formation.

In a specimen some hours older (119 hours, fig. 2), the auditory vesicle has grown much larger, and its distance from the eye has considerably diminished. The dorsal placode (*so.p.*) has markedly increased rostrad, almost reaching the level of the posterior edge of the eye. At the middle of this placode, on its ventral side, an additional placode has appeared pointing rostro-ventrad (*io.p.*), this being the first primordium of the infraorbital line. Now, the otic placode (*o.p.*) has entirely separated from the supraorbital placode, without being otherwise changed.

At the next stage (fig. 3), which is but slightly older, viz. 120 hours, marked changes have taken place. The supraorbital placode has split into two separate placodes the anterior of which will form the origin of those parts of the supraorbital line that lie in the caudal part of the frontal bone, while the posterior one constitutes the primordium of the anterior head pit-line. The infraorbital placode (*io.p.*) has moved somewhat to the ventral side, being now entirely independent of the supraorbital one. Similarly, the otic placode has separated still more from the last-mentioned placode. Caudally and ventrally to the primordium of the spiracle (*spir.*), the epithelium has begun to thicken slightly, while the cells have as yet failed to arrange themselves in a manner characteristic of the placodes. This is the first indication of the preopercular placode (*po.p.*). From statements below it will be evident that the primordium of the mandibular line does not form part of this placode.

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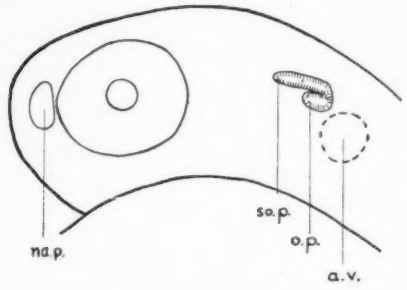

Fig. 1. *Leuciscus rutilus*, 116h. Lateral line placodes of head. 50 ×. (For lettering, see p. 125.)

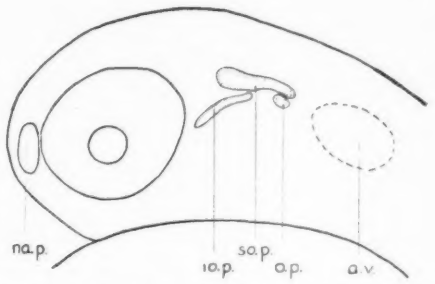

Fig. 2. *Leuciscus rutilus*, 119h. Lateral line placodes of head. 60 ×.

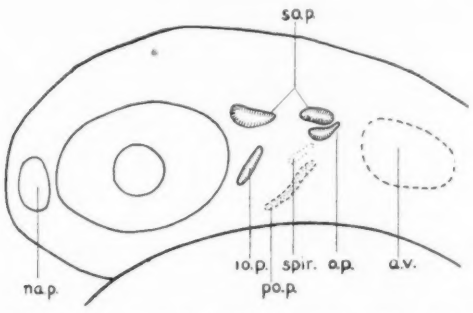

Fig. 3. *Leuciscus rutilus*, 120h. Lateral line placodes of head. 60 ×.

At the *141 hour stage* (fig. 4) further changes have occurred. Some new placodes have appeared, while those already in existence have considerably increased in length. In the supraorbital area an additional placode is to be found, on a level with the anterior part of the eye. In this placode two organs have already begun to differentiate, though they are still connected by thickened epithelium. In this new placode the anterior frontal and nasal neuromasts will originate. The supraorbital placodes, described at the previous stage, remain in the same place as before without having undergone any change. However, on account of the marked growth of the auditory vesicle frontad, the hindmost of these placodes and the otic placode have been pressed apart, being now still more separated.

The infraorbital placode (*io.p.*) has grown out under the eye, reaching, with its anterior part, almost as far as up to the nasal placode (*na.p.*). Ventrally to this still another placode has arisen, independent of the infraorbital placode. In *Salmo* similar conditions are found. In that fish the infraorbital placode forms below the eye and, when reaching its anterior edge, it markedly thickens, forming two branches in the same position as in *Leuciscus*. Also in *Amia* (Beckwith 1907), the infraorbital placode in a larva, one day old, was forked

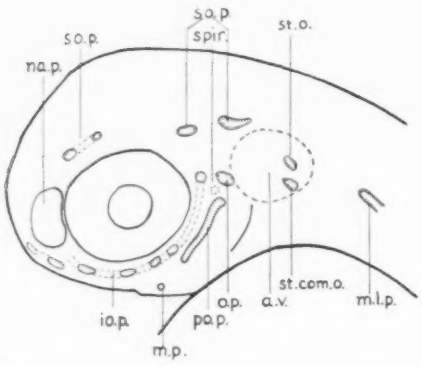

Fig. 4. *Leuciscus rutilus*, 141h. Lateral line placodes of head. 50 ×.

in its anterior part. In *Leuciscus* the anterior branch forms the origin, inter alia, of the rostral pit-commissure and the foremost sense organs in the infraorbital canal.

In this connection a conspicuous difference in the growth of the placodes, as between *Leuciscus*, on the one hand, and *Salmo* and *Amia*, on the other, should be noted. In the latter the placodes form one continuous line, gradually splitting into neuromasts. In *Leuciscus* a line of separate placodes are formed. The supraorbital line may be cited as an instance. In the last-mentioned fish this line is formed from three mutually independent placodes in which the nasal, frontal and "parietal" neuromasts, respectively, are formed. The first-mentioned type of formation is, no doubt, the most frequent one. It has been thus described, in *Selachia* and *Batoidea* by HOLMGREN (1940), and others, in *Dipnoi* by PEHRSON (1949), in *Acipenser* by NEUMAYER(1932). The latter type, on the other hand, is known in Amphibia (KNOUFF 1935, and others). As far as can be judged, this latter type of formation occurs secondarily in more specialized animal forms, easily derivable from the first-mentioned type. So far, however, the number of fishes, studied in this respect, is too limited to justify any conclusions on the basis of available facts.

At this stage, seven neuromasts have developed in the infraorbital placode. This placode at first appears as one single big organ. However, gradually distinct neuromasts differentiate in it, while the parts of the placode between the neuromasts degenerate into a thin epithelial cord, observable also in adult specimens. This epithelial cord has been noticed by many authors, and interpreted in widely divergent ways. In the adult *Ficrasfer* EMERY (1880) describes epithelial canals between the organs. MERKEL (1880) refers to a modified epithelium, suggesting that it may constitute the remainder of a degenerated canal. BODENSTEIN (1882) gives an account of a similar formation in *Cottus*, mentioning that it extends from the centre of one organ to that of another. However, this does not apply to such Cyprinids as have been

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examined. There it extends from the edges of the organs. This fact, as will be shown later, possesses a certain significance with regard to the formation of the canal bones. SOLGER (1880) describes "a side organ chain" in *Acerina* and *Lota,* consisting of "marrowless nerve fibres enclosed in a nucleated sheath". LEYDIG (1895) states that this formation is not composed of nerve fibres but of epithelial cells that encompass a cavity and may be regarded as lymphatic canals. In the Macrurids PFÜLLER (1914) noted a fine canal parallel to the lateral line, which he called canalis parallellus. Finally, as early as in 1898, CLAPP gave an interpretation which, in the opinion of the present author, is correct, as follows: "Whatever the function may be, its origin from the sense organ rudiment is not to be doubted."

The preopercular epithelial thickening, described at the preceding stage, has, at the present stage, developed into a well delimited placode (*po.p.*) which extends rostro-ventrad from the rudimentary spiracle towards the mandible. Its dorsal part turns slightly caudad. Medially on the mandible, close to the future mandibular symphysis, a neuromast (*m.p.*) has appeared without any connection with the preopercular placode. The neuromast is the foremost organ in the future mandibular line. It has been formed independently, not being severed from the preopercular placode. In *Salmo* the last-mentioned placode grows continuously as far as up to the end of the mandible, to differentiate only later into one mandibular and one preopercular line.

Near the posterior part of the auditory vesicle, two organs have appeared, one situated on a level with the ventral part of the auditory vesicle, the other with the angle between the primordia of the horizontal and the vertical semicircular canals. These organs are innervated by the glossopharyngeal nerve or the vagus. At this early stage of development, no distinction can possibly be made between these two nerves. Still, the later development shows that the upper of these organs (*st.o.*) is the one innervated by the glossopharyngeal nerve in the supratemporal bone, which develops at a far later stage, while the lower one (*st.com.o.*) forms part of the lower portion of the supratemporal commissure innervated by the vagus. Caudally to the auditory vesicle, on a level with the horizontal myoseptum, a placode (*m.l.p.*) has arisen from which, in due course, the lateral line of the body will issue.

At the *5.9 mm stage* (191 hours, fig. 5), no considerable changes have occurred. Here, the infraorbital placode has not developed to the same extent as at the previous stage. As a matter of course, this does not indicate any regressive development, since the placodes, as has often been shown, form and develop differently in relation to one another, without any absolute parallelism. In the supraorbital line yet another organ has appeared rostrally to the former ones, medially to the nasal placodes. This is the anterior nasal organ. The preopercular placode, wholly undifferentiated in its previous stage, has now begun to divide into two. One is to be found in the ventral part of the original

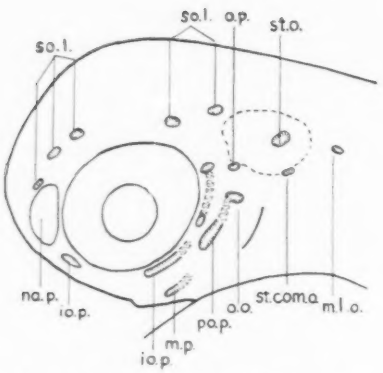

Fig. 5. *Leuciscus rutilus*, 5.9 mm. Lateral line placodes of head. 50 ×.

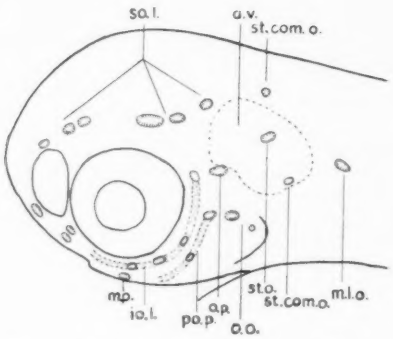

Fig. 6. *Leuciscus rutilus*, 6.3 mm. Lateral line placodes of head. 50 ×.

placode. It will form the origin of preopercular organs only. Likewise, in the original dorsal part there lies a well delimited placode, in a right angle to the original placode. This dorsal placode will, later, grow caudad and, in its anterior part, give rise to the uppermost organ in the preopercular line, and, in its caudal portion, to the opercular organs.

As far as the other organs are concerned, the two ones innervated by the glossopharyngeal nerve and the vagus have separated because of the migration caudad of the lower organ.

At the *6.3 mm stage* (247 hours, fig. 6), some of the previously described organs have divided into several ones, while some entirely new elements have appeared. Thus, the supraorbital organ, on a level with the posterior edge of the eye, has divided into two organs. Because of the pronounced growth of the mandible, the mandibular organ has moved forwards, and, in this connection, also the preopercular placode has extended a great deal forwards. In comparison with the previous stage, the upper part of this placode has grown caudad on the gill-cover. Three organs have differentiated from this placode. The foremost of these organs will in time become the uppermost organ in the preopercular line, while the two posterior ones (*o.o.*) will form part of the opercular lines. At this stage still another organ has appeared dorsally to the supratemporal organ. This new organ will later form part of the upper portion of the supratemporal commissure (*st.com.o.*).

At the *6.6 mm stage* (fig. 7), no pronounced changes have taken place. One or two observations should, however, be noted. The otic placode has split into two organs (*it.o.*), an anterior big and a posterior small one. Further, on the gill-cover the hindmost organ has grown markedly dorsad. One organ, which eventually will initiate the upper horizontal opercular line, is just being detached. The lower of the organs will, together with the one situated rostrally to it, form part of the vertical opercular line. The organs innervated by the

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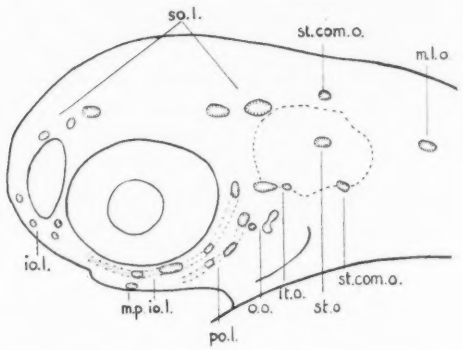

Fig. 7. *Leuciscus rutilus*, 6.6 mm. Lateral line placodes of head. 50 ×.

glossopharyngeal nerve and the vagus have separated still more, while the lower organ has continued its movement backwards.

At the *7.3 mm stage* (fig. 8), all organs are well developed, and the intermediate portions of the original placode are, at this stage, much reduced. Fundamentally, no considerable changes have occurred, apart from the fact that some new organs have appeared, supplementing I already existing lines. Since this stage brings a phase in the development of the lateral line system to a termination, as all now formed organs, with one exception, have originated from placodes, I propose to add a brief account of the conditions at this stage. The supraorbital line (*so.l.*) consists of eight organs. The three anterior ones, lying medially to the nasal placode, constitute the nasal organs. The others lie in a comparatively straight line above the eye, extending backwards to the anterior half of the auditory vesicle. The hindmost of these organs will in due course give rise to the neuromasts which later will be found in the prolonged supraorbital canal, i.e. the homologue with the anterior head pit-line organs in other fishes. The other organs in this line form the frontal organs proper. The infraorbital line (*io.l.*) consists of seven organs. In connection with the movement of the nasal placode, the two foremost organs, which are to form part of the antorbital pit-line, have changed their place and are now situated ventrally to this placode. Broadly speaking the other organs in the line remain where they have been formed. The organs innervated by the otic nerve (*it.o.*), which will eventually form part of the intertemporal bone, are situated on a level with the anterior ventral part of the auditory vesicle. At this stage the third organ in the future temporal canal[1], viz. that innervated by the glossopharyngeal nerve (*st.o.*), has occupied a peculiar position in relation to the two others. It is situated almost dorsally to the hindmost otic organ,

[1] The term temporal canal is here applied to that portion of the canal that, in the adult, will be situated in the intertemporo-supratemporal bone, the neuromasts of which are innervated by the otic and the glossopharyngeal nerves.

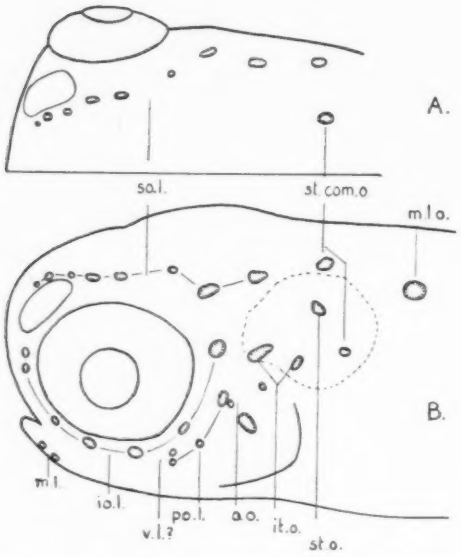

Fig. 8. *Leuciscus rutilus*, 7.3 mm. Lateral line system of head. A: dorsal view. B: lateral view. 50 ×. The sense organs joined to denote pit-lines.

in the same place in relation to the semicircular canal as described before. However, on account of the pronounced growth of the auditory vesicle, marked changes will occur in this region and, consequently, the three organs will gradually form in a straight line. The preopercular line (*po.l.*) still consists of three organs only. A fourth organ (*v.l.?*) has been added dorsally to the foremost one, but where this organ belongs, I am not now in a position to decide. Possibly it pertains to the vertical pit-line. The mandibular line (*m.l.*) consists of two organs situated in the neighbourhood of the mandibular symphysis. As compared to earlier stages, yet another organ has appeared here, caudally to the already existing one. It is worth noting that this line, unlike the preopercular one, develops from the front backwards. These lines will eventually meet at the quadrato-mandibulary joint. As to the opercular lines they still consist of three organs. The future vertical line is formed by two organs, a small dorsal and a large ventral one, which will later give rise to the rest of the vertical line, as well as to the lower horizontal line. The third organ belongs to the upper horizontal line. Finally, as to the organs innervated by the vagus, there are, at this stage, three such organs to be found, one, dorsolaterally, which will eventually form part of the upper portion of the supratemporal commissure (*st.com.o.*), another on a level with the posterior part of the auditory vesicle, which will form part of the ventral portion of the same commissure, and, lastly, a big organ belonging to the main lateral body line (*m.l.o.*).

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In the fully developed fish, all the neuromasts, so far mentioned, apart from the opercular ones, and the organ in the vertical line will become canal neuromasts, which in time will actively participate in the formation of the canal bones. The number of neuromasts does not, at this stage, agree with that of the organs in the future canals. However, they will continue to divide and give rise to both canal neuromasts and pit-line organs. Such organs as are formed, at an early stage, directly from the placodes, and, for the most part, to be found, later, in the canals, will here be termed primary neuromasts. On the other hand, such organs as will form part of pit-lines will either arise from primary neuromasts or appear wholly independently, at a late stage of development, without disclosing any signs of a previous placode formation. These organs are never to be found in canals. They will be called here secondary neuromasts. As previously shown, the opercular organs have appeared through a budding from primary neuromasts, being thus secondary. Unlike the other secondary organs, they are formed extremely early during the ontogenesis. The reason of this may be the early formation of the operculum. At this stage of development few dermal bones have formed, viz. the dental, maxillary, operculum and cleitrum. The last-mentioned is formed first, then the operculum and, some time later, the others. The operculum is developed early during the ontogenesis, always in immediate connection with one of the opercular organs. Now, the operculum does not constitute a canal bone but an ordinary dermal bone, formed from the same blastema as the hyomandibular bone (HOLMGREN 1943), yet, the first primordium of the bone always appears in close contact with one of the opercular organs. The organ may possess an inductive capacity of initiating the ossification.

All primary neuromasts need not necessarily be found in canals. This generally applies to the rostral pit commissure in the majority of Teleosts and to the anterior head line of pits in, as far as known, all recent fishes apart from the Cyprinids. In fishes without sensory canals, such as *Cobitis taenia, Corydoras* and others, all primary neuromasts will, as a matter of course, remain in the epidermis. However, late during the phylogenetic development, these primary neuromasts have been canal organs. Thus, a rostral canal commissure exists in the Ganoids and in primitive Teleosts, such as *Clupea pilchardus* (WOHLFAHRT 1937). In the Cyprinids generally, the anterior head line of pits appears as a canal, while in other Teleosts, as far as known, it remains in the skin as a pit-line, though consisting of primary neuromasts, e.g., *Salmo*. In the Paleoniscids such invagination of the anterior pit-line in a canal was a general occurrence.

At the *8.1 mm stage* (fig. 9), already existing lines have been supplemented by new sense organs, while various new lines are forming. Also the general shape of the head has changed. In particular, the nasal part and the mandible have grown markedly in length. Also, the dorsal line of the profile has assumed

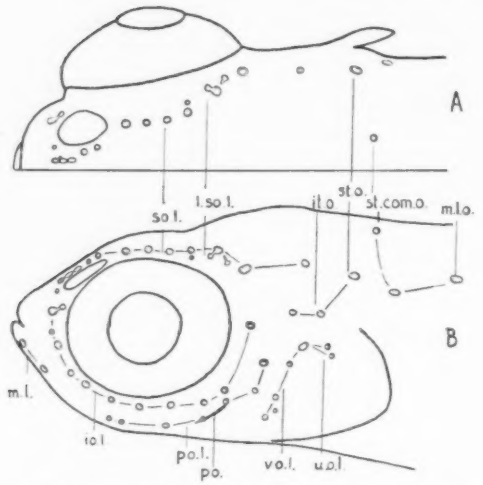

Fig. 9. *Leuciscus rutilus*, 8.1 mm. Lateral line system of head. A: dorsal view. B: lateral view. 40 ×. The sense organs joined to denote pit-lines.

another shape. Further, the gill-cover has extended backwards. In the supraorbital line a number of organs have appeared, probably through a division of previously existing ones. In addition, the organs on a level with the posterior edge of the eye, are about to form a line on the lateral side. This new line, for which the term of the *lateral supraorbital line* may be proposed (*l.so.l.*), here consists of three sense organs. The foremost one is completely detached from its mother neuromast, while the two posterior ones still remain more or less closely connected with their common one. Gradually, this new pit-line will bend down, caudally to the eye, in the direction of the posterior part of the infraorbital line and the anterior part of the temporal line. In most fishes the supraorbital canal will here, instead, curve towards the infraorbital and temporal canals. In *Salmo*, for instance, the organs in the posterior part of the supraorbital canal and the anterior pit-line develop from placodes. Thus, the neuromasts are primary. However, in *Leuciscus*, no primary neuromasts are to be found here, but only secondary ones. For this reason, the organs of the lateral supraorbital line are not, as far as can be seen, homologous with the organs in the posterior part of the supraorbital canal, in *Salmo*.

Similarly, in the infraorbital line the organs have increased in number. The foremost organ, which primarily arose from the anterior branch of the infraorbital canal, is here about to divide into two organs. The caudal organs will form part of a pit-line that, in older specimens, will extend from the anterior part of the infraorbital canal dorsocaudad, between the posterior nasal opening and the anterior edge of the eye. The preopercular line which consists of seven organs, has grown considerably rostrally, reaching almost as far as up to the

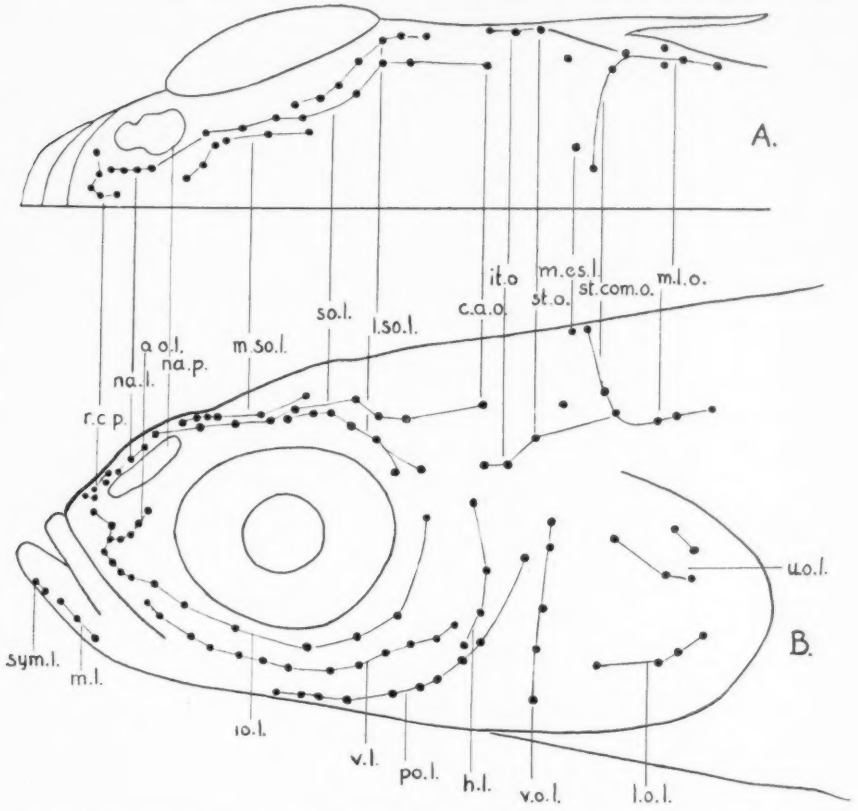

Fig. 10. *Leuciscus rutilus*, 14 mm. Lateral line system of head. A: dorsal view. B: lateral view. 40 ×. The sense organs (black dots) joined to denote pit-lines.

mandibular joint, while, on the other hand, in its posterior upper part, it has not notably developed. The vertical opercular line which, at the previous stage, consisted of two neuromasts only, situated obliquely one behind the other, has now reached its definitive extent, being composed of five organs, The lower horizontal line is still lacking. As compared to the previous stage, the vertical opercular line has palpably changed its orientation, owing to the fact that, as the nasal and the maxillary portion develop forward, the whole material on the ventral and ventrolateral side is moved frontad. As will be shown later, this is of considerable significance with regard to the interpretation of certain lines on the cheek. Further, mention may be made of the fact that both the neuromast innervated by the glossopharyngeal nerve and the middle vagus-innervated one have pronouncedly moved backwards in relation to the otic organs.

At the *14 mm stage* (fig. 10), a further great number of neuromasts have appeared, though as yet no trace is to be discerned of the formation of any canals. Since the innervation of the organs can be determined with a fair

amount of certainty and since the dermal bones are well developed, the different lines can be definitely ascertained.

Medially to the eye three lines occur. The original supraorbital line, viz. the medial one, extends from the anterior edge of the nasal placode to the level of the anterior edge of the auditory vesicle. It consists of two clearly distinguishable parts, viz. an anterior nasal one, medially to the nasal placode, and a posterior frontal part. Medially to the anterior half of the frontal part, a new line has appeared composed of six organs. Its anterior part bends towards the medial line. In all the examined Cyprinids, this line is more or less well developed, and I shall propose to call it the *medial supraorbital line* (*m.so.l.*). Whether this line has originated from a division of the primary supraorbital line, or wholly independently, is difficult to decide. However, I have been unable to ascertain any signs of division at any of the intermediate stages and, in addition, certain circumstances, in connection with the innervation in the adult (see page 24), suggest that it may be an independent line. Laterally to the caudal part of the supraorbital line, the lateral line that, at the previous stage, was forming has gained independence and now consists of seven organs. In its anterior part it is parallel with the original line, while, behind the eye, it turns downwards in the direction of the upper part of the infraorbital line.

Especially in its rostral part, the infraorbital line (*io.l.*) has markedly developed, some new organs being formed. Because of the comparatively great number of new organs and the rapidity of the development during this phase, no minute analysis has proved possible with a view to arriving at a conclusion regarding the exact origin of the different organs, i.e. whether they have developed independently or from a division of some already existing organs. The anterior part of the infraorbital line is forked. One branch (*r.c.p.*) runs rostrally to the nasal placode. On the dorsal side it meets the corresponding branch from the opposite side, i.e. the rostral pit commissure. The other branch (*ao.l.*) runs dorsocaudad towards the posterior edge of the forementioned placode. For this line, described in *Esox* by PEHRSON (1944 a), I suggest the name of the *antorbital pit-line*, since, at least as far as the Cyprinids are concerned, it is always connected with the antorbital bone. The last-mentioned line and the rostral commissure have originated from the anterior branch of the infraorbital placode (fig. 4). From this placode also the two foremost organs in the infraorbital line derive. These two organs, as well as the sense organs in the antorbital and rostral lines are primary neuromasts. In Teleosts they generally remain in the epidermis as pit-lines. In *Amia* (PEHRSON 1922, fig. 16) the same bifurcation is met with in the infraorbital canal. The rostral part of the canal constitutes the rostral commissure, while the caudal pit-line branch in *Leuciscus* corresponds to the part of the infraorbital canal in *Amia* that contains neuromast 5. Also in *Clupea pilchardus* (WOHLFAHRT 1937) these two branches are found to correspond to canals.

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In the mandibular line three organs have appeared. In the mandible two lines can now be distinguished, viz. a rostromedial line, i.e. the symphysial line (*sym.l.*, SANZO 1911), and, caudally and laterally to this line, the mandibular line (*m.l.*). On the gill-cover the lower horizontal opercular line (*l.o.l.*) has developed, while the corresponding upper line (*u.o.l.*) is doubled. On the cheek two additional well developed lines have appeared, viz. an almost vertical line (*h.l.*), situated between the posterior part of the infraorbital line and the preopercular line. As will later be clearly demonstrated in *Nemachilus*, this line constitutes the "horizontal pit-line", with an orientation entirely differing from the usual one in Teleosts. The other of the new lines extends from the lower half of the forementioned line towards the nose, collaterally with the infraorbital line, i.e. "the vertical pit-line" (*v.l.*). These two last-mentioned lines are not formed by division of previously existing lines, nor from any previously discernible placode. The organs issue directly from a seemingly indifferent epithelium. These lines began to form, differentiating at one and the same time in their whole length already in a slightly younger specimen. Finally, at this stage still another line has begun to form, immediately in front of the uppermost organ in the supratemporal commissure. This line has probably, arisen through a separation from a primary organ. Considering the genesis and position of the line, just in front of the canal in the adult, it can hardly be a "posterior head pit-line". This line is, as a rule, situated more rostrally and, as far as known, it has no connection with the organs in the supratemporal commissure. JARVIK (1948), found in *Osteolepis* a line immediately in front of the canal commissure, which he called "the pit-line of median extrascapulars" and, in addition, certain lines further along the parietal bone. With regard to its position, the first-mentioned line corresponds to the forementioned line in *Leuciscus*.

At this stage, all lines, except the accessory preopercular and accessory infraorbital pit-lines which develop very late, have formed. However, already existing lines are further developed by means of a formation of additional organs, particularly in the vertical line.

B. The origin and development of the canals.

The first signs of the canals can be observed in an 18 mm long specimen. Certain of the primary neuromasts begin to sink in the epidermis, each in a special pit. Simultaneously, the epithelium has begun to thicken, especially between the organs, projecting like a massive keel into underlying tissues. This description applies to the nasal neuromasts in the supraorbital line, as well as to the anterior frontal ones in the same line, up to the level of the middle of the eye. The caudal part of this line still remains completely unchanged. Between the nasal and frontal parts of the line the epithelium is, also, unchanged. Thus,

these two parts form independently of one another. In the infraorbital line no changes are as yet noticeable. In the anterior and posterior parts of the mandibular line a similar epithelial thickening can be observed, while the medial part of the line remains as before. Thus, the dental and the angular parts of the canal are formed separately, from the front backwards. The preopercular line offers the same picture. In the anterior part of the line, just behind the mandibular joint, the canal has already begun to sink in. Further back, the canal becomes more shallow, gradually being transformed into a thickened epithelium, while, in its posterodorsal part, remaining completely unchanged. Thus, the mandibulo-preopercular canal is formed in three places, viz, at the dental bone, the angular bone and at the anterior part of the preopercular bone. In all three instances the formation sets in rostrally, continuing backwards, until all the three canals have joined. As yet, there is no indication of the other canals.

In a 20 mm long specimen, the anterior portion of the frontal part of the supraorbital line has become invaginated, and a closed canal containing a neuromast has arisen. Similarly, in the anterior part of the preoperculum a short canal has developed.

In a 22 mm long specimen the rostral part of the frontal canal has closed a little more. It now contains three neuromasts. The nasal part of the canal, as well as the mandibular canals, are unchanged. The preopercular canal has entirely closed, except its posterior part. The extension of the future infraorbital canal now begins to manifest itself through a slight epithelial thickening, best developed in its antorbital part. No trace is as yet to be noted of the other canals.

In a 26 mm long specimen the anterior part of the infraorbital canal has begun to sink in, though without as yet closing. The outline of the temporal canal and of the dorsal part of the supratemporal commissure has become descernible in the shape of a slight epithelial thickening. (As regards details of the development of the canal from this epithelial thickening, see *Phoxinus*).

At the *44 mm stage* (fig. 11), the canals have for the most part already formed or are about to form. Since the lateral line system will not after this be subjected to any particularly marked changes, I shall choose this stage as illustrative of the condition also in adults.

C. The lateral line system in the adult fish.

(Figs. 11, 12.)

Organs innervated by the ophthalmicus superficialis VII.

This nerve innervates the organs of the supraorbital canal and certain pit-lines connected with this canal.

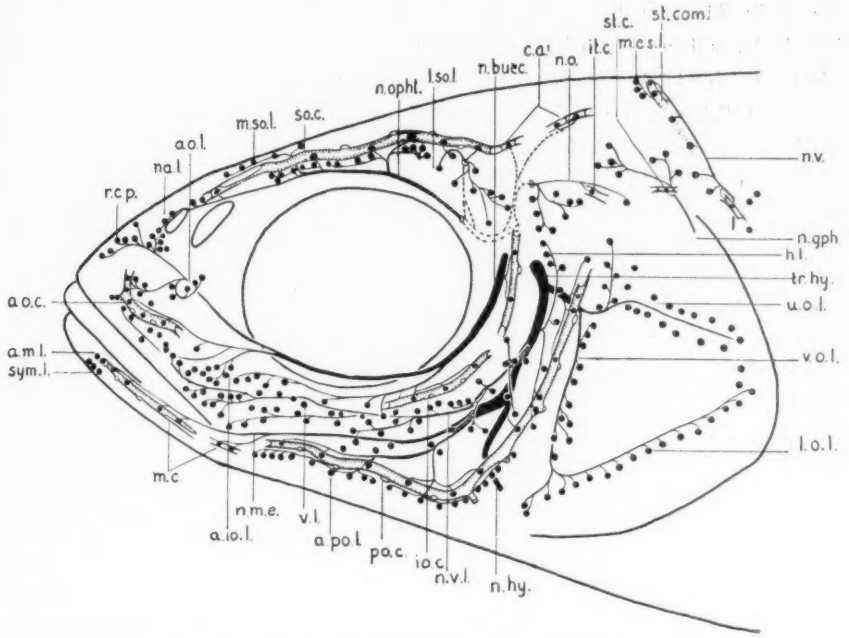

Fig. 11. *Leuciscus rutilus*, 44 mm. Lateral line system of head. 12 ×.

The supraorbital canal (*so.c.*) begins medially to the nasal openings, continuing backwards in a straight line medially to the eye. At the posterior edge of the eye, the canal turns laterad, then, after a sharp, clearly accentuated angle, it makes its way on the dorsolateral side of the head over the parietal bone terminating in front of, and close to, the supratemporal commissure. Three portions can be distinguished in this canal, viz. a nasal and an anterior and a posterior frontal part. The anterior frontal part extends from the anterior edge of the frontal bone to the forementioned angle. The two anterior portions form early and independently of one another. However, the posterior part sinks in very late, as a direct continuation of the middle part. The two anterior canal parts are innervated by extracranial branches of the ophthalmicus superficialis while the posterior portion is innervated by intracranial branches of the same nerve. At this stage the nasal and anterior frontal parts have fused, but the boundary between these two parts still remains marked by a long open furrow. At this stage, the nasal part of the canal contains only one neuromast. However, immediately in front of the canal there is another organ which in older specimens will also be included in the canal. Thus, there are in most cases two nasal organs, but, occasionally, as will be seen from fig. 42, an additional organ will be found in the left nasal bone. The anterior frontal part has three neuromasts, the posterior frontal and the parietal parts three and two organs, re-

spectively. Thus, in the entire supraorbital canal altogether ten organs are to be found. As will be shown later, the supraorbital canal of this fish, like that of other examined Cyprinids, discloses a course differing from that of other examined Teleosts, e.g. *Salmo, Esox* and many others. In fishes generally, this canal curves downwards behind the eye, joining the infraorbital and temporal canals. In *Leuciscus* no such connection is to be found. There, the canal continues straight caudad over the parietal bone. DEVILLERS (1944 c and 1947) discussed this question and, like the present author, he arrived at the conclusion that the prolonged canal part is homologous with the anterior head pit-line. For this reason, DEVILLERS termed this part "canal antérieur". In, e.g., *Salmo,* which the present author has been in a position to study, the anterior head pit-line is composed of primary neuromasts, formed from a placode that is a direct continuation of the supraorbital placode. In this fish, however, the organs are not invaginated in a canal, but remain as a pit-line. Thus, the way of formation is in these two fishes identical, while the final result in *Leuciscus* is a canal, in *Salmo* a pit-line. Further, DEVILLERS states that the organs of the "canal antérieur" are innervated by the otic nerve, i.e., the same nerve that innervates both the intertemporal organs and the forementioned neuromasts. However, in the specimen analysed in the present paper, the otic nerve and the nerve of the organs in the "canal antérieur" are separate. In my opinion, the last-mentioned nerve is an intracranial branch of the ophthalmic nerve. Also, DEVILLERS draws attention to the fact that MANIGK (1933), described a common "otic canal antérieur nerve" in *Phoxinus,* but that he himself, in specimens of the same fish, found that these nerves may be separate. In my view, everything seems to indicate that the organs of the "canal antérieur" are innervated by the ophthalmic nerve and that its fusion with the otic nerve is secondary. In addition, DEVILLERS discusses the question where the boundary should be drawn between the frontal canal proper and the "canal antérieur". To begin with, the opinion that first suggested itself to him was that the part where the organs were innervated by the "N. oticus" should be considered to constitute the "canal antérieur", but later, after his observations in *Phoxinus,* as related above, he found some difficulties in arriving at a conclusion in this way and, for this reason, he left the matter open, stating: "En resumé, nous parlerons, chez *Leuciscus,* d'un canal supra-orbitaire prolongé jusque sur le Parietal par un canal antérieur, mais sans décider où finit l'un ou commence l'autre." Evidently, the innervation can give, no definite answer to this problem. On the other hand, I believe that the embryological development can offer certain clues. Embryologically, the supraorbital line originated from different placodes, the posterior part of the future canal, i.e. the part behind the forementioned angle, arising from an independent placode. Further, this part of the canal became invaginated extremely late as compared to the parts in front. Here, therefore, are two facts indicating that the part lying

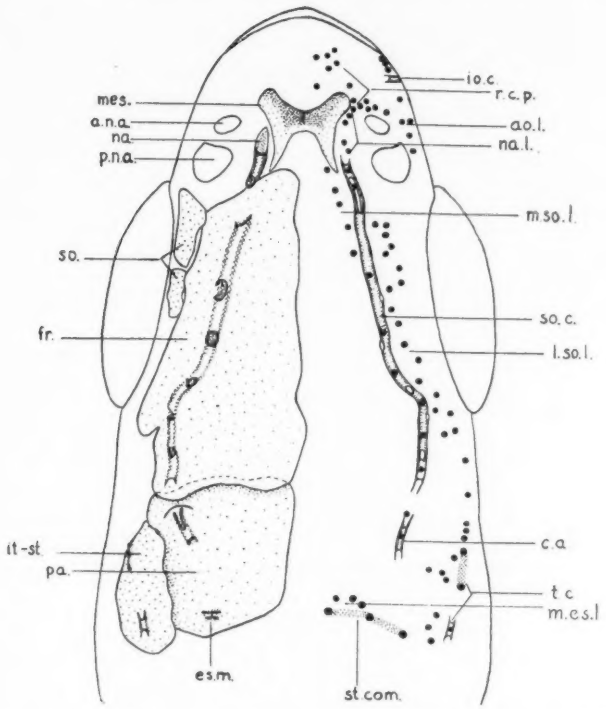

Fig. 12. *Leuciscus rutilus*, 44 mm. Head from dorsal side. Bones on left side, lateral line system on right side. 12 ×.

behind the angle differs from the rostral parts, both as regards the earlier and the later ontogeny. Thus, in my view, the boundary between the two canal elements is to be found at the forementioned angle.

Apart from the neuromasts in the canal, also a number of free organs are innervated by this nerve. The supraorbital canal is continued rostrally by a short pit-line (*na.l.*), running rostrally and medially to the anterior nasal opening. This nasal pit-line (PEHRSON 1945) seems to be comparatively frequent in fishes. PEHRSON describes it in *Gymnarchus* (1945) and *Polypterus* (1947). JARVIK (1947) has given an account of the same line in *Polypterus* under the name of "the tectal pit-line". Among the Cyprinids it occurs generally. In *Gymnarchus* it was supposed to originate as a differentiation of the nasal part of the supraorbital line. Observations in *Leuciscus* and other investigated fishes confirm this contention. This is particularly obvious in *Phoxinus*. In my account of this fish I shall, therefore, return to this question. Medially to the anterior part of the supraorbital canal runs a line of five organs, i.e., the medial supraorbital line (*m.so.l.*), innervated by one and the same nerve branch. Especially in young specimens this line tends to form a

commissure. Between the eye and the canal is another considerably longer line, the lateral supraorbital line (*l.so.l.*), that turns downwards behind the eye in the direction of the posterior upper part of the infraorbital canal. This line is innervated by different branches of the ophthalmic nerve. As shown above (fig. 9), this line developed from primary neuromasts. Consequently, the neuromasts have the same innervation as their mother neuromasts and, being innervated by different branches, also the separated organs will be innervated by the corresponding branches. On the other hand, as far as the medial line is concerned, it was stated, in the description of its ontogeny, that its origin has proved untraceable. No division had been noticed. The whole line is innervated by a nerve branch which runs exclusively to this line but not to any canal neuromasts. From this the conclusion might be drawn that the line has developed wholly independently. Evidence such as the relation between the small nerve branches and various kinds of neuromasts may not justify any far-reaching conclusions, but together with other facts it can, no doubt, be cited as a fairly good indication.

Organs innervated by the nervus buccalis VII.

This nerve innervates both the neuromasts in the infraorbital canal and a number of independent organs in the nose and under the eye.

The infraorbital canal (*io.c.*) is, at this stage, incomplete, and composed of three different canals which, in older specimens, may fuse into one canal, extending from the point of the nose to the vicinity of the temporal canal. The foremost of the three portions of the canal lies on the antorbital bone and includes five organs. The canal is semicircular, beginning with a pore directed dorsad. The pore between the organs 2 and 3 is directed forwards. As regards the innervation of these organs, they are all innervated by the buccal nerve, the two anterior ones, however, by another branch than the others. On a level with the middle of the eye, the buccal nerve bifurcates, the upper of the two branches innervating the rostral pit-commissure (*r.c.p.*), the antorbital line (*ao.l.*) and the two above-mentioned most rostral canal organs. In the examined Cyprinids, these three groups of organs are constantly innervated by one and the same buccal branch. This seems to apply to most Teleosts and is particularly striking in *Esox* (Pehrson 1944 a), as well as in *Clupea* (Wohlfahrt 1937). On the other hand, in *Amia* (Allis 1889) and *Polypterus* (Pehrson 1947) the position differs. Here, small branches, one to each neuromast, issue from the buccal nerve. Embryologically, the two forementioned pit-lines and the two canal neuromasts have arisen from a common placode, viz. the anterior branch of the infraorbital placode (fig. 4). The number of organs is great, but it has emerged that, if for some reason or other a primary neuromast is not invaginated, it often divides into a number of neuromasts. This is particularly

usual and extremely marked in, e.g. the Gobiids. Thus, in *Gobius niger,* which, inter alia, lacks an infraorbital canal, the neuromasts in the infraorbital line are found to have split into transverse lines with up to ten organs per line. In all likelihood, the same course of development has occurred in the case of the rostral pit-commissure and the antorbital line. Since these lines ontogenetically consist of primary neuromasts, they might have been expected to have become invaginated in canals. In Teleosts generally this is a rare occurrence. Only in the more primitive *Clupeids* is a developed rostral canal to be found (WOHLFAHRT 1937). In the *Ganoids,* on the other hand, this is the rule. As to the antorbital line, it may occasionally become a canal. This applies, e. g., to *Clupea pilchardus.* Further, this line is probably homologous with the upwards pointing antorbital branch of the infraorbital canal in *Amia,* comprising organ No. 5 (ALLIS 1889). In *Leuciscus* this branch is but rather slightly developed, while in other Cyprinids, as will be shown later, it may be considerably longer and, occasionally, between the nose and the eye, form a commissure with a meeting line innervated by the ophthalmic nerve.

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Apart from the antorbital portion of the canal, two parts of the canal are to be noticed, one under the eye, another behind it. Gradually, though comparatively late in the development, these three canals fuse. In all examined Cyprinids, this canal develops exceedingly late, particularly the part situated on a level with the first infraorbital bone. In the whole canal system this part is, constantly, the last to develop, in striking contrast with the conditions in *Nemachilus,* as will be demonstrated later. The posterior canal elements contain three and two organs, respectively. Between the anterior and the middle canal there are five primary neuromasts which will later be invaginated. When fully developed, the infraorbital canal thus lodges about 15 neuromasts.

Along the anterior two thirds of the infraorbital canal a number of free neuromasts are to be found, invariably lying ventrally to the canal. In certain Cyprinids these neuromasts form a pit-line, parallel with the canal. In *Leuciscus* they are more irregularly situated. They are innervated by buccal branches. At a late stage of development, immediately before the formation of the canal, these organs have developed from the organs in the primary infraorbital line. I propose that they be termed *the accessory infraorbital line* (*a.io.l.*). Unfortunately, I have been unable to ascertain definitely the innervation of the accessory organs below the antorbital part of the canal, because of the fact that buccal nerves are here mixed with nerves that innervate the horizontal pit-area of the cheek.

Organs innervated by the truncus hyoideo-mandibularis.

Branches of this nerve innervate both the organs of the mandibulo-preopercular canal and a number of pit-lines in the cheek and the gill-cover.

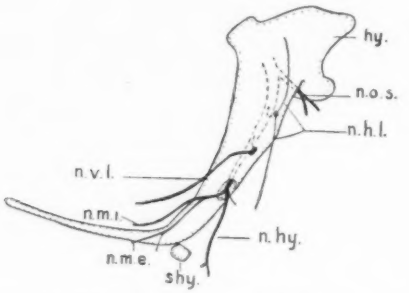

Fig. 13. *Leuciscus rutilus*, 44 mm. Left hyomandibular bone and truncus hyoideo-mandibularis with its branches. 12 ×.

In the course of its passage through the hyo-mandibular bone, the trunk emits a number of lateral branches, each passing through a separate foramen in this bone (fig. 13). Proximally, one branch issues which passes through a foramen on the posterior edge of the hyo-mandibular bone, innervating lines on the gill-cover, i.e. the superficial opercular nerve (*n.o.s.*). Distally, another branch appears, which, after having passed through its foramen, divides into a dorsal and a ventral branch, constituting nerves to the horizontal pit-line (*n.h.l.*). Finally, there is a further branch which, likewise, passes through the bone, viz. the branch to the vertical pit-line (*n.v.l.*). After having passed through the hyo-mandibular bone the nerve bifurcates into the hyoid and mandibular nerves, the latter in its turn dividing into two branches, viz. the internal mandibular nerve (*n.m.i.*) and the external mandibular nerve (*n.m.e.*), running, respectively, inside and outside the mandibular arch. The latero-sensory fibres follow the external branch.

In this specimen the mandibulo-preopercular canal consists of three different canals, the two anterior ones belonging to the mandibular canal (*m.c.*). The foremost one lies in the dental-splenial bone, containing four neuromasts. The posterior canal, which, at this stage, is but a furrow, has two organs situated in the angular-splenial bone. The preopercular canal (*po.c.*) runs in an even curve from the mandibular joint up to the temporal canal, ending slightly ventrally to this. The canal contains ten organs, with an additional one in older specimens, to be seen on the surface directly dorsally to the upper part of the canal. The upper part of this canal develops extremely late. The six foremost organs are innervated by the external mandibular nerve, the seventh organ by a branch of the hyoid nerve and the three (four) last ones by branches of the opercular nerve. In short, chiefly the ventral part of the preopercular canal may be said to grow, whereas the dorsal portion does not develop any further.

A vertical pit-line (*h.l.*) of about ten organs is parallel to the upper part of the preopercular canal. As will be shown later, this vertical line is, in

Nemachilus, identical with the horizontal pit-line. As will be seen from the previous description of the ontogeny of this line, it forms comparatively late, occupying from the first the same position and extent as in the adult specimen. Consequently, the embryology provides no clues for an interpretation. In *Nemachilus*, on the other hand, the line develops extremely early, extending from the beginning horizontally from the upper edge of the preopercular line towards the infraorbital line. In the course of the further development pronounced changes of position take place at the side of the head, which gradually cause the originally horizontal line to assume a vertical position. An horizontal line (*v.l.*) that in *Leuciscus* extends from the preopercular canal, between that canal and the infraorbital canal, towards the nose, is subjected to the same change in position. In *Leuciscus*, there is no marked line to be noted. It may rather be regarded as a "pit-field". In *Nemachilus* this line forms, to begin with, as a vertical line which, gradually, bends forwards into a more horizontal position. The nerve that innervates this horizontal pit-field leaves the trunk through a hole in the hyomandibular bone and, after having passed straight through a portion of the musculus adductor mandibulae, it runs subcutaneously. This nerve, here termed "the nerve to the vertical line", is met with in the literature under many different names. Thus, HERRICK (1901) calls it "the cutaneous branch of the R. mand. ext. VII". HÜSEMANN (1919) uses the name of "R. buccalis facialis". MANIGK (1933), and others, calls it "R. buccalis accessorius". Since the last-mentioned term, which is, perhaps, the most frequent, may easily be mixed up with the accessory infraorbital line which is innervated by the buccal nerve. I have suggested the above-quoted name, viz. nerve to the vertical line. Also, the "buccalis accessorius" has nothing to do with the buccal nerve, which is sufficient reason for a change of name.

Collaterally with the horizontal part of the preopercular canal runs a pit-line, originating from the preopercular line, and innervated by the same branches of the external mandibular nerve that innervates the canal neuromasts. The line extends towards the mandibular joint. This line forms extremely late. It has developed from the primary canal neuromasts in a specimen 20 mm long, just before the invagination of the canal. The line is typically secondary and I suggest "*the accessory preopercular line*" as a name for it.

Also, ventrally to the anterior end of the mandible a short pit-line of three organs is to be noted, innervated by the external mandibular branch, viz. the symphysial pit-line (SANZO 1911). This line seems to be exceedingly frequent in Teleosts. Thus, it is found, in a more or less well developed state, in all examined Cyprinids, as well as in the Gobiids (SANZO 1911). PEHRSON (1945) described a similar line in *Gymnarchus* under the name of "the anterior mandibular line of pits", and also, in 1947, in *Polypterus*. Further, the same author in 1944 gave an account of a similar line in *Esox*, consisting of a number of small organs situated in a direct line from the mandibular canal, comparing

these organs with the anterior mandibular line in *Gymnarchus*. However in *Gymnarchus* this line lies medially to the mandibular canal and, for this reason, it cannot be homologous with the above-described line in *Esox*. Actually, this is a matter of two entirely different lines, both found in the Cyprinids, on the one hand a medial line close to the mandibular symphysis, i.e. the symphysial line, on the other a line constituting a direct continuation of the mandibular canal, the anterior mandibular line. As pointed out by PEHRSON, the last-mentioned line has originated from primary mandibular organs that have not been invaginated in canals. The other line forms quite independently at an early stage of the development. As will be shown later, it differs in appearance from one Cyprinid to another.

On the gill-cover, there are three pit-lines, viz. the vertical (*v.o.l.*), and the upper (*u.o.l.*) and lower (*l.o.l.*) horizontal opercular lines. All are innervated by branches of the superficial opercular nerve. This nerve divides into two branches, the upper of which innervates the upper line, while the lower branch innervates the vertical and lower horizontal line. The two horizontal lines converge towards the posterior edge of the gill-cover where they meet. In this fish, unlike other examined Cyprinids, the upper line is doubled.

Organs innervated by the otic nerve.

This nerve innervates the two intertemporal neuromasts, as well as a number of free sense organs. The nerve issues from the dorsal side of the trigemino-facial ganglion, fusing, after a short passage, with an ophthalmic branch which, likewise, issues from the dorsal side of the same ganglion, just in front of the first-mentioned nerve. For a short way the two nerves run together, being, nevertheless, wholly distinguishable. After that the otic nerve passes through a foramen in the sphenoticum. Thus, in this fish, as well as in the other examined Cyprinids, and in *Nemachilus*, this nerve is intracranial, passing the cranium through a foramen of its own. In the Silurids (HERRICK 1899) "this nerve (to quote his own words) has an independent origin from the extra-cranial portion of the ganglionic complex". The nerve, then, runs rostrad and dorsad between the cranium and m. levator arcus palatini. In the Gobiids the nerve leaves the cranium through the foramen of the trigeminal nerve. In *Esox* (PEHRSON 1944 a) it is extracranial. The same applies to *Amia*. Thus, this nerve runs differently in the Cyprinids than in other examined fishes.

After the passage through its foramen the nerve divides into two branches, one ventral, innervating a number of neuromasts irregularly distributed rostro-ventrally to the temporal canal. These organs have not to my knowledge been described in any other Teleosts. In the Cyprinids they are always found, more or less numerously. In the Gobiids there are, as I have observed, in this area one or more free neuromasts, innervated by the otic nerve. For the present I

am not in a position to interpret these organs in detail, nor have I succeeded in analysing their ontogeny. They may, possibly, be homologous with a spiracular line, innervated by the otic nerve, to be found in a great many primitive fishes and in the Dipnoi (HOLMGREN—PEHRSON 1949). The other otic branch runs caudad, innervating the two intertemporal canal neuromasts. At this stage the canal is not fully developed. Round the anterior organ the canal has sunk in, though still remaining unclosed, while round the posterior organ so far only an epithelial thickening is noticeable, indicating the future extent of the canal. In the Cyprinids there are two canal neuromasts innervated by the otic nerve, unlike the Silurids which, constantly, seem to have only one.

Organs innervated by the glossopharyngeal nerve.

This nerve, which leaves the cranium through a small foramen immediately in front of that of the vagus, innervates an organ in the temporal canal, as well as a number of free neuromasts dorsally to this canal. This part of the canal, viz, the supratemporal (*st.c.*), arises independently of both the intertemporal portion of the temporal canal and the main canal of the body. These three components will fuse only very late. The free organs innervated by this nerve lie in two groups dorsally to the canal, the one above the intertemporal and the other above the supratemporal part. Whether any of these groups correspond to the middle pit-line of the head is difficult to say. In the Gobiids there are organs innervated by the glossopharyngeal nerve in exactly the same place but, in addition, a well developed, similarly innervated pit-line is to be found on the dorsolateral side, in my opinion probably the middle head line of pits. Thus, a comparison between these two fishes would disclose the absence of a middle pit-line in *Leuciscus*.

Organs innervated by the vagus lateralis.

This nerve innervates the organs in the supratemporal commissure, as well as the line in front of it. The nerve issues from the extracranial portion of the lateralis X-ganglion. The supratemporal commissure is composed of seven organs. At this stage the canal is as yet not fully developed. The two dorsal organs lie in a furrow, the others remain superficial, while being connected by a thickened epithelial cord. Immediately rostrally to the dorsal commissural organs lies a short line of three organs, viz. the median extrascapular line (*m.cs.l.*), innervated by the same vagus branch which runs to the canal neuromasts. In all probability, this line has developed from the primary upper canal neuromasts.

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3. THE LATERAL LINE SYSTEM IN *PHOXINUS PHOXINUS* L.

The lateral line system was fully dealt with by MANIGK in 1933. He chiefly analysed the trigemino-facial complex and the innervation of the neuromasts of the head. Also, in a couple of illustrations he shows the position of the organs and the canals. He has, however, not examined the ontogenesis, nor has he made any comparisons with other fishes. In his survey of the canal system he very rightly states that the number of sense organs and pores in the canals varies considerably. This explains the occasional lack of conformity between MANIGK's pictures and those of mine. Also v. WOELLWARTH (1933), who examined the neuromasts in this fish was able to confirm the occurrence of great variations, observing "dass die Herkunft der Tiere für die Entwicklung der Seitenlinie offenbar eine Rolle spielt, denn Tiere gleicher Herkunft zeigten oft auffallende Ähnlichkeit im Zustand ihrer Seitenlinie". Since MANIGK's specimens, in all probability, derive from the South of Germany, while those of mine come from the North of Sweden, this would in itself suffice to explain certain dissimilarities. Apart from the forementioned author, also DYKGRAAF (1934), has produced an illustration of the lateral line system. though his picture is schematic, and he does not enter into any discussion of its morphology. Finally, STENSIÖ (1947), has reproduced one of MANIGK's pictures, adding certain re-interpretations of the lines.

A. The postembryonic development.

In a 7.3 mm long specimen (fig. 14), which discloses a striking conformity to the 8.1 mm stage in *Leuciscus* (fig. 9), the neuromasts have differentiated from the placodes, the latter having been reduced to a fine epithelial cord between the organs. As in the case of *Leuciscus*, only the primary neuromasts are, on the whole, formed, while the secondary ones, but for a few opercular organs, are entirely missing. Thus, the supraorbital line (*so.l.*) consists of ten organs, the three foremost ones, medially to the nasal placode, being nasal and the three next frontal, while the last one, which lies considerably caudally to the others, dorsally to the temporal organs, will form part of the prolonged supraorbital canal(*c.a.o.*). In the adult, 8—10 organs are to be found in the supraorbital canal. Immediately rostrally to the first nasal organ lies yet another organ which, as far as can be judged, will in due course form part of the rostral pit-commissure (*r.c.p.*). The infraorbital line (*io.l.*), which in front of the eye bends sharply dorsocaudad, between the nasal placode and the eye, is composed of twelve organs. In the adult, there are 11—12 organs in the corresponding canal. As in *Leuciscus*, the mandible lodges only one neuromast (*m.l.*), situated rostrally on it. This is the foremost organ in the mandibular line. Fig. 16 shows how the number grows by the addition of new organs, caudally to the first one. The preopercular line (*po.l.*) begins at the mandibular

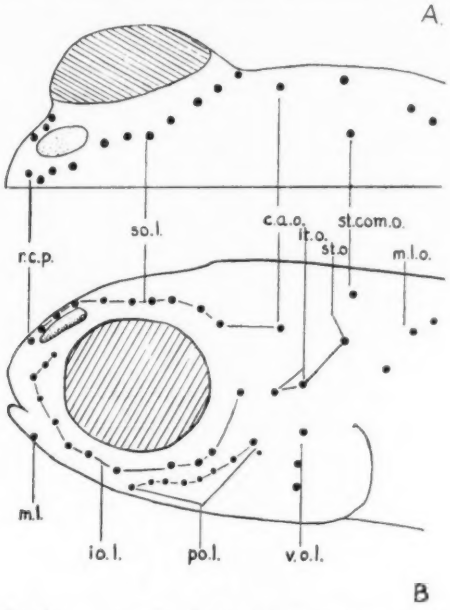

Fig. 14. *Phoxinus phoxinus*, 7.3 mm. Lateral line system of head. A: dorsal view. B: lateral view. 40 ×. The sense organs joined to denote pit-lines.

joint, extending from there dorsocaudad towards the temporal organs and ending a good way below these organs. Further, there are two intertemporal organs (*it. o.*) and a supratemporal one (*st.o.*), in the same mutual position in relation to one another as in *Leuciscus*, as previously described. In the course of the following development these three organs will occupy a straight line. Finally, some organs innervated by the vagus are to be seen, the uppermost of which will in time be found in the supratemporal commissure. All the organs now referred to are primary. As in *Leuciscus*, at this young stage only a few secondary organs are to be noted, viz. the opercular ones. Thus, on the gill-cover there are three organs in a vertical row (*v.o.l.*), the vertical opercular line. Otherwise, no pit-lines have formed. During the following development a great many neuromasts will, however, appear, almost exclusively secondary ones.

In a specimen only slightly older (9.4 mm, fig. 15) the neuromasts have increased in number, and new lines have been added. Already at this stage certain difficulties, in sorting out the organs, are met with. At older stages this becomes unfeasible, until the specimens are old enough to render the innervation definitely ascertainable. In the supraorbital line a number of organs have, at this stage, appeared. The distribution of the organs of this line is no longer so regular as at the preceding stage. The three nasal organs are easily recognizable, but in the frontal part of the line a number of organs have arisen,

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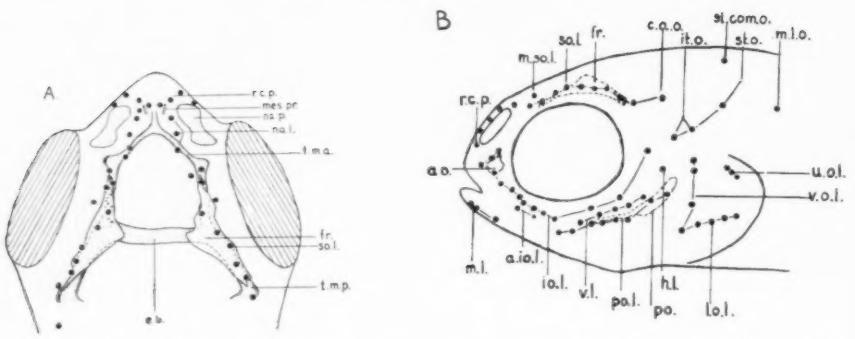

Fig. 15. *Phoxinus Phoxinus*, 9.4 mm. Lateral line system of head. A: dorsal view, 33 ×. B: lateral view, 25 ×.

constituting the first primordia of the medial and lateral supraorbital lines, respectively. In fig. 15 a the frontal bone has been drawn. On it six or seven neuromasts lie, while the organs situated outside the bone belong to the forementioned lines. The infraorbital line (*io.l.*) retains, on the whole, the same appearance as before. Below three of the anterior organs an antorbital bone has developed. An examination of several specimens indicates that the most rostral organ will not be situated above the bone, but will be included in the rostral pit-commissure (fig. 16). Below the seven posterior organs of the preopercular line (*po.l.*) the preoperculum has formed (*po.*). The line reaches as far as to the vicinity of the mandibular joint. Between this line and the infraorbital line a new line has appeared, comprising five organs, viz. the vertical pit-line (*v.l.*). Whether or not the most caudal organ (*h.l.*) should be said to belong there is difficult to determine. However, as a comparison with *Nemachilus* will show, this organ is likely to pertain to the horizontal line. On the gill-cover two new lines are discerned, viz. the upper and the lower horizontal line. Intermediate stages disclose that the upper line has originated from the uppermost of the three organs that were to be found in the 7.3 mm stage, while the lower line derives from the ventral of these organs.

In older specimens the secondary pits pronouncedly increase in number and, as stated above, the identity of the organs will defy definition, unless the innervation can be conclusively ascertained. This particularly applies to the cheek, as the different lines here fuse into one single large pit-field. However, in other places, for instance on the dorsal side, the development of the various lines can be more easily analysed. As an instance, the nasal line (figs. 17 a—d) may be mentioned. In a 27 mm long specimen this region only holds the three nasal organs and the rostral pit-commissure. When, in older specimens, the nasal bone has formed, only two of the three organs will be found to lie in that bone. The foremost organ, on the other hand, will give rise to the nasal line. In a 35 mm long specimen the line is well developed, but the number

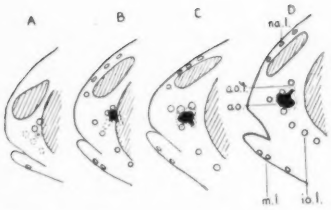

Fig. 16. *Phoxinus phoxinus*. Development of the antorbital bone. A: 7.9 mm. B: 8.3 mm. C: 8.9 mm. D: 9.4 mm, 33 ×.

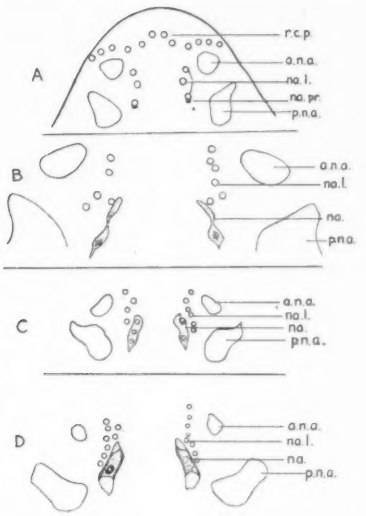

Fig. 17. *Phoxinus phoxinus*. Development of nasal bone and nasal line of pits. A: 27 mm, 14 ×. B: 35 mm, 25 ×. C: 47 mm, 10 ×. D: 60 mm, 10 ×.

of organs increases with age, at least before a length of 60 mm has been attained. From this instance it will be seen that the number of neuromasts increases till the fish has reached sexual maturity, and that new pit-lines will appear comparatively late in the course of the development.

B. The formation and development of the canals.

As stated in the introductory remarks, the canal system is extremely inconstant, the number of canal elements varying from one specimen to another. Even in the same individual the number of canal elements on the right side may differ from that on the left side. Also, the time of the formation of the canals varies. Thus, there is a specimen of 40 mm (from the vicinity of Stockholm) in which the mandibular canal is fully developed, while in another specimen of 47 mm (from the North of Sweden) the anterior part of the same canal is just about to sink in. However, common to all examined specimens is that the mandibular canal is the first to be formed and, also, that it begins to sink in rostrally, then continuing caudad. Simultaneously, also the preopercular canal will be formed. Only after the completion of these canals will the supraorbital canal form and, much later, the infraorbital canal will appear. The temporal canal and the supratemporal commissure appear approximately at the same time as the supraorbital canal. Unlike most examined fishes, in this one the canals remain unconnected, i.e. divided into a number of canal portions,

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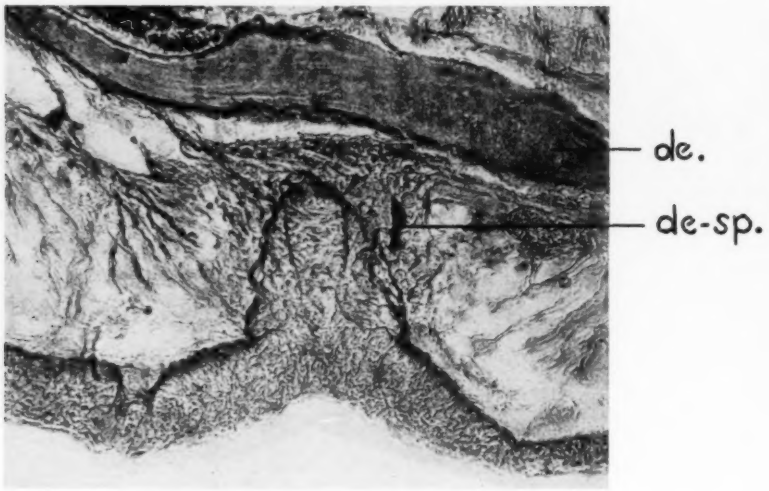

Fig. 18. *Phoxinus phoxinus*, development of mandibular canal, 47 mm. Microphoto 350 ×.

each portion often containing only one single neuromast. However, a fusion of these portions will occur, and from this process canals of a varying length result. In *Leuciscus* the canals were, likewise, to a large extent formed as separate parts with, usually, one organ in each canal, but in that fish the different elements fused and continuous canals gradually appeared. In *Phoxinus* this fusion partly fails to appear and, consequently, also the fully developed fish exhibits a row of separate canal elements. Also with regard to the formation of the canals, this fish differs in certain respects from those previously described. Normally, the canals in Teleosts will originate from an invagination of the epithelium into a broad furrow which will then close. Thus, a canal with a wide lumen will form. In *Phoxinus*, the canals—at least those that appear first, i.e. the mandibulo-preopercular canal—are formed in a somewhat different way (figs. 18, 19). Just before the canal is about to sink in, the deeper parts of the epithelium assume the shape of a small massive ridge and, secondarily, a lumen will appear. The canals that form later, e.g., the infraorbital canal, will develop in an entirely normal way, through a wide invagination. Occasionally, this secondary lumen formation may fail to appear, and the canal, also in the adult specimen, will then be almost massive. The sensory canals in sharks form, in principle, in the first described way. ALLIS (1904) distinguishes two types of formation with regard to the canals, viz. the plagiostomian and the teleostean. "The plagiostomian canal is", he states, "the result of a dehiscence or deliquescence in the central portion of a solid cord of cells formed by an involution of the deeper layers only of the ectoderm, while the teleostean canal is the result of a much larger involution which in-

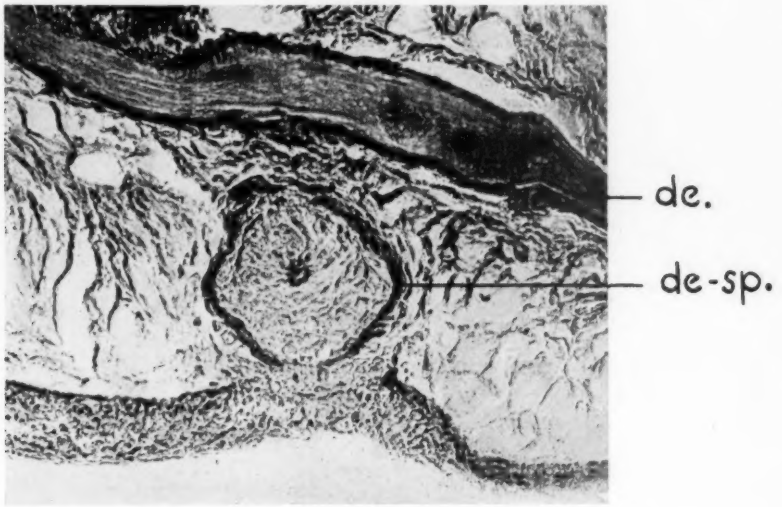

Fig. 19. *Phoxinus phoxinus*, development of mandibular canal, 47 mm. Microphoto 350 ×.

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volves the entire ectoderm and includes within it the ectodermal region that gives origin to the plagiostomian canal." He adds that the first-mentioned type is only found in the Selachoids and the Batoids, but probably also in the Chondrostei, while the latter type will be noted in the Teleostei, Holostei and doubtless also in the Crossopterygii. From ALLIS' classification and account it should be evident that both types of canal formation occur in *Phoxinus*. Also in the other examined Cyprinids this first-mentioned type of formation appears rather frequently, though more or less distinctly developed. Generally, a first sign of the formation of the canals can be traced as a clearly marked epithelial thickening projecting towards underlying tissues. Later, however, the development may turn out differently. Either this epithelial ridge will remain for a considerable time, a lumen being formed only secondarily, through a breaking-down of the central cells, or the canal formation may take place quite normally, through an invagination of a broad strip of epithelium.

C. The lateral line system in the adult fish.
(Figs. 20, 21, 22.)

As mentioned above, the lateral line system in the adult fish was described in detail by MANIGK (1933), and the results arrived at by the present author on the whole agree with his. However, MANIGK did not analyse the various lines in detail, nor did he compare them to the corresponding lines in other fishes. For this reason, I propose to submit a brief account of the system, even though this will unavoidably necessitate an enumeration of some known facts.

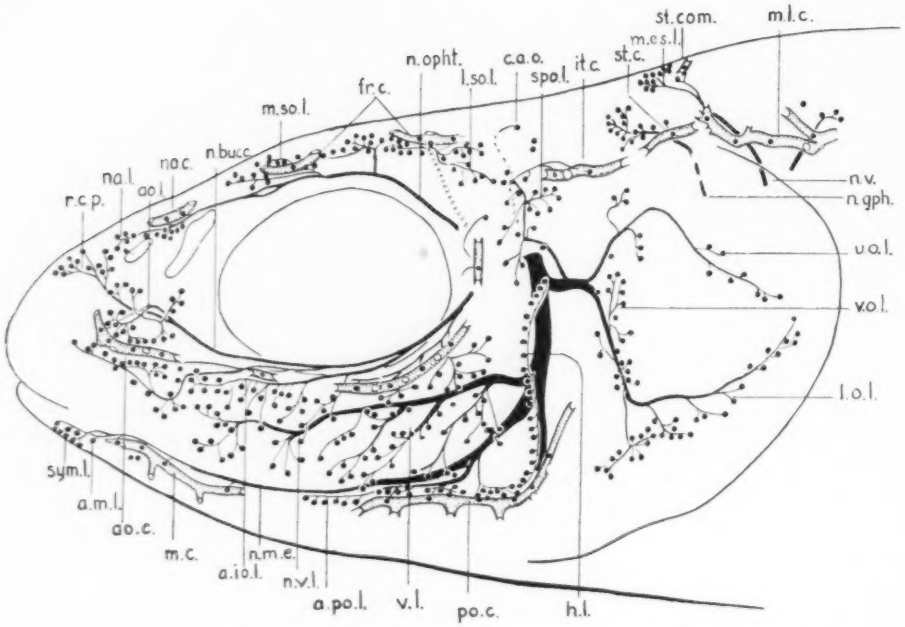

Fig. 20. *Phoxinus phoxinus*, 60 mm. Lateral line system of head. 10 ×.

In the examined specimen the supraorbital canal consists of three canal portions of which the foremost one, containing two organs, constitutes the nasal canal. The two others lie on the frontal bone. In the specimen described by MANIGK yet another portion of a canal is found, caudally to the forementioned one, corresponding to the "canal antérieur". The organs of the third canal are innervated by an independent intracranial branch of the superficial ophthalmic nerve, while the others are innervated by extracranial branches. The hindmost primary supraorbital organ, which, in the specimen examined by me, was not invaginated in a canal, is innervated by an intracranial branch of the superficial nerve which, together with the otic nerve, issues from the trigemino-facial ganglion, this in exact analogy with *Leuciscus*, apart from the fact that in *Phoxinus* the two branches have completely fused. However, as mentioned earlier, DEVILLERS (1947), has examined specimens of *Phoxinus* in which these two nerves were independent of one another.

Apart from those canal neuromasts, some pit-lines, previously described in *Leuciscus*, are innervated by this nerve. Thus, there is a nasal line, laterally and rostrally to the nasal canal. As stated above, this line was formed late in the development. Laterally to the supraorbital canal a line (*l.so.l.*) extends along the greater part of the frontal bone, curving downwards behind the eye. Medially to the anterior part of the canal, there is a faintly developed medial

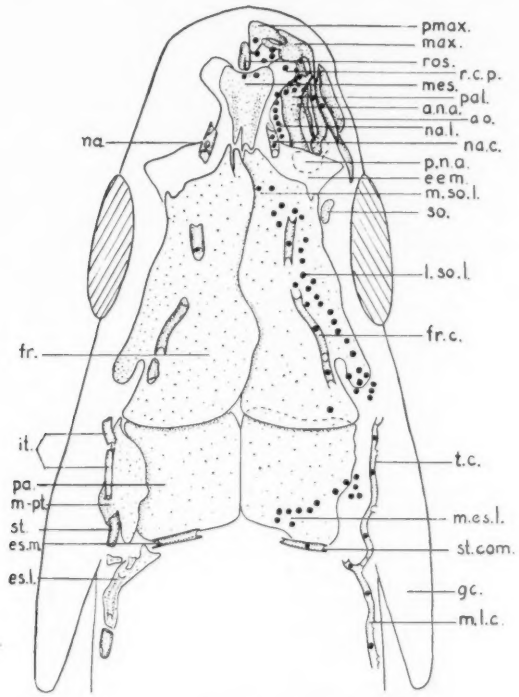

Fig. 21. *Phoxinus phoxinus*, 60 mm. Skull from dorsal side. On the right side lateral line system. 10 ×.

supraorbital line (*m.so.l.*) which, on a level with the anterior edge of the frontal bone, forms a commissure.

The infraorbital canal consists of four separate canals, one in the antorbital bone (*ao.c.*) and one in each of the three other infraorbital bones. In addition to the neuromasts in these canals, a large number of free organs are innervated by the n. buccalis VII. Thus, ventrally to the infraorbital canal, there is a considerable number of organs, corresponding to the accessory infraorbital line (*a.io.l.*) in *Leuciscus*. In the nose, an antorbital line (*ao.l.*) and a well developed rostral pit-commissure (*r.c.p.*) are to be seen. As in *Leuciscus*, the first canal neuromast, as well as these two last-mentioned lines, are innervated by a common buccal branch.

The mandibulo-preopercular canal is composed of two separate canals, viz, a mandibular one (*m.c.*) with four neuromasts, three in the dental-splenial and one in the angular-splenial bone, and a preopercular canal (*po.c.*) with six organs. The preopercular canal is extremely short, extending scarcely halfway up towards the temporal canal. The organs in these two canals are innervated by the external mandibular nerve, which also innervates a number of organs on the ventral side of the mandible, i.e. the symphysial line (*sym.l.*,

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Fig. 22. *Phoxinus phoxinus*, 60 mm. Anterior part of head from ventral side. 10 ×.

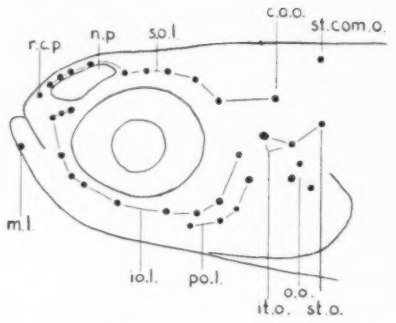

Fig. 23. *Alburnus alburnus*, 7.9 mm. Lateral line system of head. 10 ×. The sense organs joined to denote pit-lines.

fig. 20, 22). In this fish the symphysial lines on the right and left side have fused, together forming a pit-field, on the rostral point of the mandible at the anterior part of the mandibular line (*a.m.l.*), which constitutes a direct continuation of the mandibular canal. Further, the same nerve innervates an accessory preopercular line (*a.po.l.*) placed side by side with the preopercular canal.

On the cheek the two normal pit-lines, one horizontal (*v.l.*), one vertical (*h.l.*), are to be found. The horizontal line or, rather, the horizontal pit-field occupies the space between the infraorbital and mandibulo-preopercular canals. The entire field is innervated by the nerve to the vertical line. Further, there is a vertical line (*h.l.*) that forms a direct continuation of the accessory preopercular line.

On the gill-cover the three usual lines are, likewise, to be seen, all well developed. The upper and lower horizontal lines converge towards the posterior edge of the gill-cover.

Proximally to the superficial opercular nerve, another nerve branch runs rostrodorsad, innervating a number of organs between those innervated by the otic nerve and the vertical line. MANIGK states that the organs in question are innervated by the otic nerve. No doubt, certain of these organs are innervated by this nerve, but, nevertheless, many of them are innervated by the forementioned nerve. A corresponding line with exactly the same innervation is met with in the *Gobiids* and *Anguilla*. In 1911, SANZO described this line in a number of *Gobiids*, under the name of "prima serie transversale inferiore del solco oculo-scapolare", a rather awkward term for which I suggest that "the suprapreopercular line" be substituted (*spo.l.*).

The temporal canal consists of an anterior portion (*it.c.*) with two neuromasts, innervated by the otic nerve, and a posterior portion with an organ innervated by the glossopharyngeal nerve (*st.c.*). As mentioned above, the otic

nerve issues from the dorsal side of the ganglion, together with a superficial ophthalmic branch. Apart from the forementioned canal neuromasts, a number of free organs on the ventral side of the canal are also innervated by this nerve.

In addition to the above-mentioned organs the glossopharyngeal nerve (*n.gph.*) also innervates a number of free neuromasts dorsally to the canal. The supratemporal commissure (*st.com.*) is represented by a short canal with one organ. In front of this line a well developed median extrascapular line is to be seen (*m.es.l.*).

4. THE LATERAL LINE SYSTEM IN *ALBURNUS ALBURNUS* L.

(Figs. 23, 24, 25.)

To my knowledge, no description of this system exists. Because of the fact that the epithelium is extremely delicate and, consequently, easily injured, undamaged specimens have been unavailable and, for this reason, it has proved impossible to follow the development in detail.

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The conditions in a 7.9 mm long specimen (fig. 23) agree considerably with those at the 7.3 mm stage in *Leuciscus* (fig. 8), as well as with those at the 7.3 mm stage in *Phoxinus* (fig. 14). Below the eye runs an infraorbital line (*io.l*) of eleven organs. Rostrally, it bends sharply dorsocaudad between the nasal placode and the eye. The supraorbital line (*so.l.*) has four organs situated medially to the nasal placode. The organ immediately in front of the forementioned organs (*r.c.p.*) belongs to the rostral pit-commissure. Medially to the eye, the frontal portion of the line, including five organs, is to be seen and, caudally to the eye, on a level with the anterior part of the auditory vesicle, is yet another organ, which will later form part of the prolonged supraorbital canal (*c.a.o.*). The preopercular line (*po.l.*) is still not entirely formed. It consists of only four organs parallel to the posterior part of the infraorbital line. It is the middle portion of the line. The anterior and posterior parts have so far not formed. Of these two the last-mentioned portions will form first. Later, the dorsal portion of the line will develop. The mandibular line (*m.l.*) consists of one organ only, situated far in front on the mandible, in the vicinity of the symphysis. Also here the organs of the temporal line (*it.o., st.o.*) occupy the same position in relation to one another as described in *Leuciscus* and *Phoxinus*, with the supratemporal organ moved into a dorso-caudal position. The supratemporal commissure is composed of only one organ situated dorsolaterally (*st.com.o.*). The opercular lines are represented by three organs (*o.o.*), which defy any identification. As in the case of *Leuciscus* and *Phoxinus*, only primary neuromasts have formed, except the opercular organs.

In a 42 mm long specimen (figs. 24, 25), the entire lateral line system is formed, but for a few exceptions. The canals have completely sunk in and

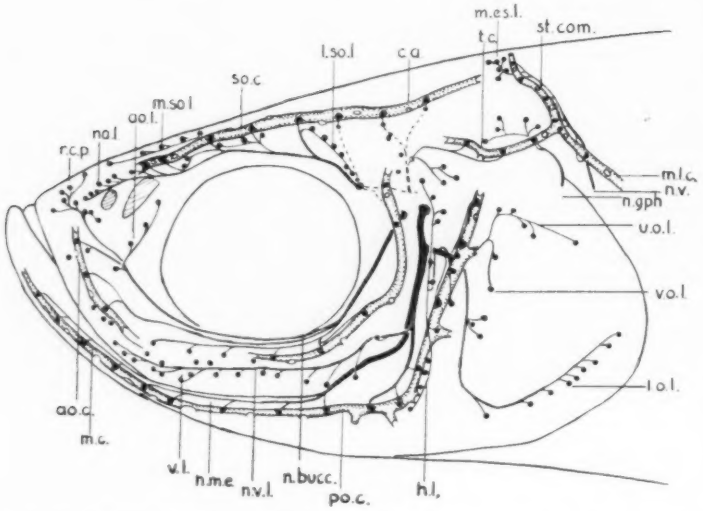

Fig. 24. *Alburnus alburnus*, 42 mm. Lateral line system of head. 13 ×.

closed, apart from a short portion of the infraorbital canal under the eye and, possibly, the anterior part of the supraorbital canal.

The supraorbital canal (*so.c.*) runs in a comparatively straight line over the eye. There it turns slightly laterad, to proceed from there caudally to the posterior edge of the frontal bone, continuing on the anterior half of the parietal. At this stage the canal is entirely continuous, though, as in the previously described species, it has formed in portions. Already in a 20 mm long specimen the frontal part of the canal begins to sink in, to be closed in a 28 mm long specimen. In the latter specimen also the nasal part of the canal has begun to sink in, in direct connection with the frontal part, in contrast with the previously described fishes, where this canal arises entirely independently. No trace is as yet to be found of the "canal antérieur". This canal forms later as a direct continuation of the frontal portion. The complete supraorbital canal contains eight organs, but immediately rostrally to the anterior part of the canal there is, in addition, a free neuromast, which participates in the formation of the nasal bone and later, in all probability, constituting an ingredient in the canal. Altogether, nine organs are to be found in the definitive canal. The three foremost of these belong to the nasal part, the three following to the frontal portion, and the three last to he "canal antérieur". The six foremost organs are innervated by extracranial branches of the superficial ophthalmic nerve, the seventh one by an intracranial branch. The two hindmost organs, the one situated on the frontal, the other on the parietal bone, are innervated by a common branch which, together with the otic nerve, issues from the dorsal side of the trigemino-facial ganglion. The two nerves run so closely together

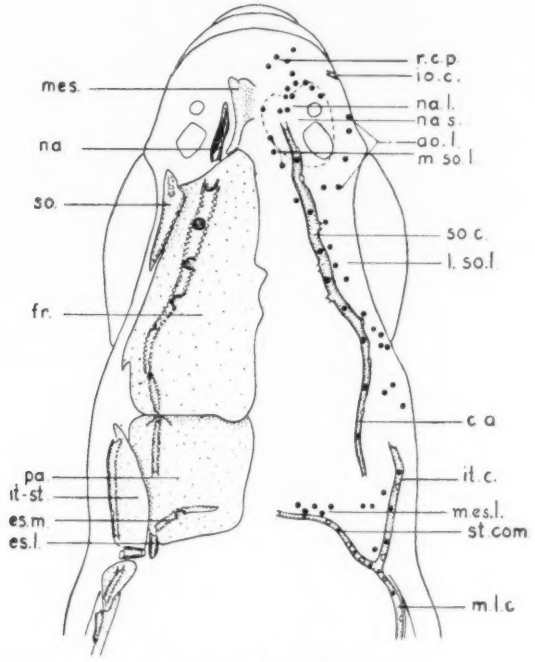

Fig. 25. *Alburnus alburnus*, 42 mm. Head from dorsal side. Bones on left side, lateral line system on right side. 13 ×.

that it is impossible to distinguish between them. However, the position here entirely conforms to that in *Leuciscus* apart from the fact that, in that fish, the nerves were clearly distinguishable. Therefore, there are reasons for assuming that also in this case two nerves are concerned, viz. a branch of the superficial ophthalmic nerve and a branch of the otic nerve, which have fused.

As in the previously described Cyprinids, the infraorbital canal is formed very late. In a 28 mm long specimen the canal has not yet begun to develop and, at the 48 mm stage, it still remains incomplete, being entirely closed in its anterior antorbital part, as well as in the posterior half, comprising the two hindmost infraorbital bones. In the region of the first infraorbital bone there is, so far, no indication of any canal. The fully developed canal contains eleven neuromasts, innervated by the buccal nerve. As in previously described species, the first organ in the canal is innervated by an independent buccal branch, which also innervates the rostral pit-commissure and the antorbital line.

The mandibulo-preopercular canal (*m.c.*, *po.c.*) forms in two different parts. Already in a 20 mm long specimen the anterior part of the preopercular canal has begun to sink in. In a 22 mm long specimen, its anterior part has closed

and is about to sink in caudad. In a 28 mm long specimen the canal is complete from the mandibular joint to, and including, the uppermost of the primary preopercular organs. Only considerably later, the dorsal part of the canal is formed. The mandibular part of the canal forms far later. In the 28 mm specimen no primordium of this canal appears. In the 42 mm specimen it is fully developed and connected with the preopercular canal. The mandibular canal lodges six neuromasts, the four foremost lying in the dental-splenial bone, the two posterior in the angular-splenial bone. The preopercular canal contains nine organs, the eight anterior in the preoperculum, while the remaining ninth, peculiarly enough, is to be found in the operculum. Altogether, the canal thus comprises fifteen organs, the nine anterior ones being innervated by the n. mand. externus, the three next by a branch of n. hyoideus and the four last by branches of n. opercularis superficialis.

The temporal canal includes the normal number of two otic organs and one innervated by the glossopharyngeal nerve. The supratemporal commissure (*st.com.*), which is connected with the forementioned canal and the main lateral canal, contains four organs innervated by the vagus.

As the previously described species, also this fish has a well developed pit-line system fundamentally of a similar appearance.

The n. opht. superf. innervates a line of six organs, situated rostrally to the supraorbital canal and constituting a direct continuation of this canal, viz. the nasal line (*na.l.*). Further, there is a line medially to the nasal part of the canal, "the medial supraorbital line" (*m.so.l.*), and, finally, one laterally to the same canal, "the lateral supraorbital line" (*l.so.l.*), which in an even curve bends down towards the upper part of the infraorbital canal.

The n. buccalis innervates the rostral pit-commissure (*r.c.p.*), as well as the antorbital pit-line (*ao.l.*), which in this species is fairly well developed, extending between the posterior nasal opening and the eye. These two lines and the upper organ in the antorbital canal are innervated by a common buccal branch, issuing far back from the nerve trunk, on a level with the posterior part of the eye. Also a number of free neuromasts, associated with the infraorbital canal, are, probably, innervated by this nerve, but owing to the fine structure of the nerve fibres, the innervation has proved unascertainable. These organs would correspond to the accessory infraorbital line in previously described fishes.

As usual, a number of lines are innervated by the truncus hyoideo-mandibularis. A proximal branch of the n. opercularis lateralis innervates, apart from the forementioned canal neuromasts, also the horizontal pit-line (*h.l.*) and the organs on the gill-cover. In *Leuciscus*, the nerve to the horizontal line issued directly from the trunk, but in this fish it follows, for a short distance, the opercular nerve. This horizontal line is almost parallel with the vertical portion of the preopercular canal towards the temporal canal. As far as the opercular lines are concerned, they are rather faintly developed, as compared

to the species previously referred to. Thus, an upper and a lower horizontal line and a but feebly developed vertical line are discernible. Distally to the forementioned nerve, still another nerve issues from the trunk, viz. the nerve to the vertical line, which, unlike the corresponding nerve in *Leuciscus*, does not leave the trunk till the main trunk has passed through the hyomandibular bone. After having run past the musculus adductor mandibulae, it continues close below the epidermis innervating a line going horizontally, viz. the vertical line (*v.l.*) which, in this fish, is less complicated than in *Leuciscus* and *Phoxinus*. It extends upwards in the maxilla, to the level of the posterior end of the antorbital canal, consisting of a number of organs situated in a straight line. Whether this fish possesses any accessory preopercular line has proved unascertainable, since all the examined specimens have been damaged in this particular region. However, such a line is most likely to exist.

Also in this place the otic nerve innervates a number of free nuromasts, situated vertically to the temporal canal. Likewise, the glossopharyngeus innervates a number of free neuromasts, dorsally to the canal. Finally, the vagus innervates the posterior pit-line, which consists of five free organs immediately in front of the supratemporal commissure.

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5. THE LATERAL LINE SYSTEM IN *ABRAMIS BLICCA* BLOCH.

(Figs. 26, 27.)

The lateral line system in *Abramis* has been dealt with by SAGEMEHL, quite casually, in 1891. He briefly described the canal system of the head.

The lateral line system in this species resembles, on the whole, that of previously discussed species. Nevertheless, there are certain dissimilarities.

The canal system is well developed and, as in the species analysed above, it reveals certain peculiar features. The supraorbital canal offers the same appearance as in *Leuciscus* and *Alburnus*, with a laterally directed curve on a level with the posterior portion of the eye. From there the canal runs towards the posterior edge of the frontal bone, and continues on the anterior half of the parietal bone. According to SAGEMEHL (1891), this prolongation of the canal would extend so far on the parietal bone as to establish connection with the supratemporal commissure. However, in the specimens examined by me, even adult ones, I have never come across such an instance. Instead, the canal has invariably terminated in the middle of the parietal bone, at a short distance in front of the commissure. The entire canal includes fifteen organs, viz. four in the nasal bone, nine in the frontal and two in the parietal, i.e. a considerably greater number than in the previously described species. Each organ is, in an entirely normal way, placed between two pores. The pore tubes in front of the curve are directed laterad, those situated in the actual curve mediad, while, finally, the hindmost organs again point laterad. As will later be seen from the

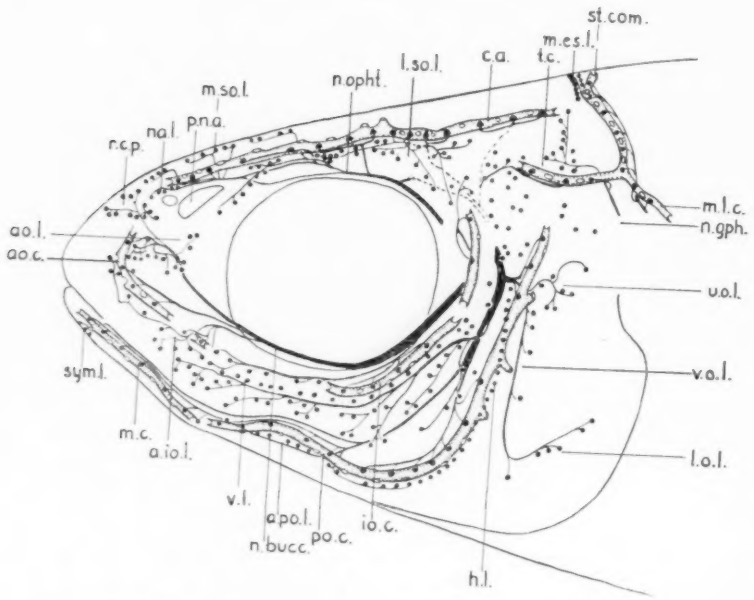

Fig. 26. *Abramis blicca*, 40 mm. Lateral line system of head. 10 ×.

general discussion, this canal with its pores reveals striking similarities to the corresponding canal in the Paleoniscids. The innervation of these canal neuromasts differs somewhat from that of the previously described species and, at first sight, appears somewhat bewildering in comparison. As earlier pointed out by STANNIUS (1849), with regard to *Tinca*, the n. ophthalmicus V and VII are, from the beginning, separate from one another, leaving the cranium each through a foramen of its own (figs. 26, 41), while in *Leuciscus* and *Phoxinus*, the two nerves went together, issuing jointly through one foramen. In this fish the two nerves fuse immediately outside the cranium. The organs in the nasal and frontal portions of the canal are innervated by extracranial branches of the n. opht. superficialis VII, while the hindmost organs in the frontal bone, as well as the organs in the "canal antérieur", are innervated by intracranial branches. As in *Alburnus*, the nerve that innervates the three hindmost organs issues in conjunction with the otic nerve.

As in the already analysed species, the infraorbital canal in *Abramis* remains incomplete. In the examined specimen it consists of four canal portions, one in each infraorbital bone. Rostrally lies a curved canal (*ao.c.*) in the antorbital bone, lodging four organs. In the anterior part of the first infraorbital bone there is a short canal with one organ. In the whole of the second infraorbital bone a long canal with four organs is to be noted. The same applies to the third bone, where two organs are included. Between the first and second por-

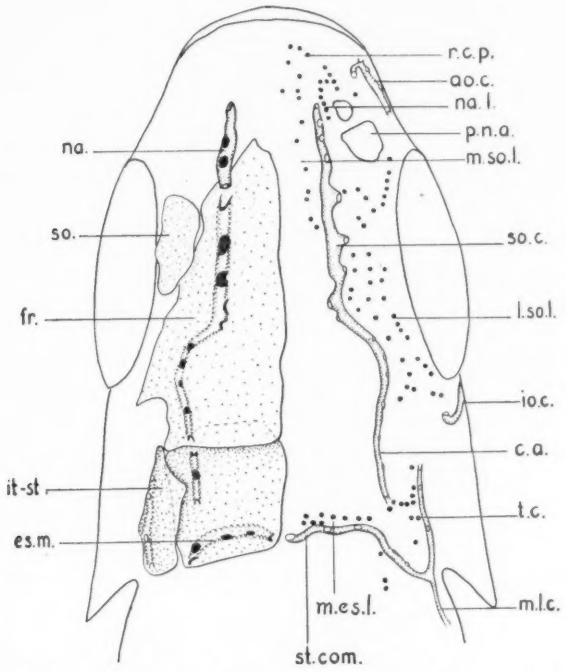

Fig. 27. *Abramis blicca*, 40 mm. Head from dorsal side. Bones on left side, lateral line system on right side. 10 ×.

tions of the canal lies a free neuromast, and between the second and third canal parts six neuromasts, which, in older specimens, when the canal is complete, turn into canal neuromasts. All together, eighteen organs will belong to the infraorbital canal. All are innervated by the buccal nerve VII. Also in this species, the foremost canal organ is innervated by a buccal branch that, in addition, proceeds to the rostral pit-commissure and the antorbital line.

The mandibulo-preopercular canal consists of two different portions, viz. a mandibular (*m.c.*) and a preopercular (*po.c.*). The boundary between them lies at the mandibular joint. The anterior canal contains six organs, the posterior fourteen. The ten foremost organs are innervated by n. mand. externus, the seven next by a branch from the R. hyoideus and the three hindmost by branches of the n. opercularis lateralis.

The temporal canal, the supratemporal commissure and the main lateral canal agree entirely with those in *Leuciscus* and *Alburnus*.

Like the previous species, *Abramis* has an extremely developed pit-line system, fundamentally agreeing with that in the previously described fishes, though differing from it in certain details.

The superficiai ophthalmic nerve innervates a great many free neuromasts

on each side of the supraorbital canal. Thus, laterally to the canal, and medially to the anterior nasal opening, a short line of five organs appears, viz. the nasal pit-line (*na.l.*). Further, there is a line medially to the nasal canal and the anterior part of the frontal canal, viz. the medial supraorbital line (*m.so.l.*). Laterally to the canal, a well developed line (*l.so.l.*) is seen. In the previously examined species this line has been comparatively simple, but in this species the number of organs has greatly increased and, in the first place, the term pit-field suggests itself, even though certain parallel lines may be observed in it. Thus, such a line bends ventrad between the posterior nasal opening and the eye, meeting the antorbital line that issues from the opposite direction. Behind the eye the lateral line curves towards the upper portion of the infraorbital line.

Among the lines innervated by the buccal nerve, also here the rostral pit-commissure (*r.c.p.*) and the antorbital line (*ao.l.*) are to be seen. Together with the first infraorbital canal neuromast they are innervated by one common branch. Also an accessory infraorbital line (*a.io.l.*), parallel with the canal, is noted. Also in this fish it has in this instance proved difficult to determine the innervation.

As regards the lines innervated by the n. hyoideus-mandibularis, the position is identical with that previously described. Apart from some neuromasts the n. opercularis lateralis innervates also the three opercular lines which, in this particular case, owing to the exceptional shortness of the gill-cover, is rather feebly developed. Further, note is to be made of a well developed horizontal pit-field (*v.l.*) and a vertical line (*h.l.*), parallel with the upper part of the preopercular canal. This line is continued forwards to the mandibular joint through an accessory preopercular line (*a.po.l.*). In addition, there is a short symphysial line of three organs on the ventral side of the mandible (*sym.l.*).

The organs innervated by the otic, glossopharyngeal and vagal nerves agree exactly with the corresponding organs in the previously described species.

6. THE LATERAL LINE SYSTEM IN *TINCA TINCA* L.

(Figs. 28, 29.)

The lateral line system in this fish has been described by ANDRES (1899), but his paper has not been available in Sweden and, for this reason, I have been unable to pay regard to it. ALLIS (1904), in referring to *Tinca* states that "it seems to present exactly the same arrangement as in *Moxostoma*". "No mandibular canal is", according to ALLIS, "given in this fish (Tinca), this confirming its absence in *Moxostoma.*"

Like the previously described species, also this fish presents an exceedingly well developed lateral line system with canals and a great many free neuromasts arranged in lines, i.e. not in more or less diffuse pit-fields.

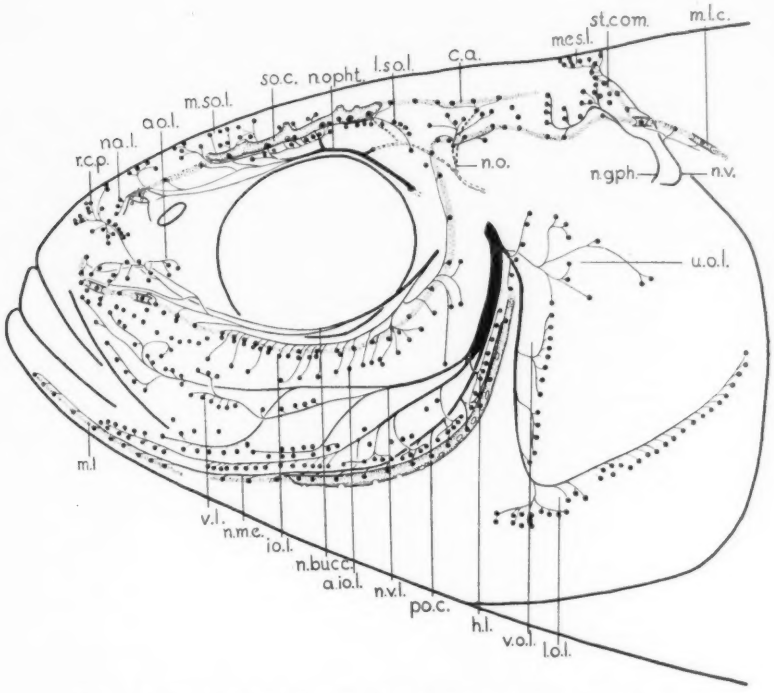

Fig. 28. *Tinca tinca*, 46 mm. Lateral line system of head. 11 ×.

In the examined 46 mm specimen, the canals are, so far, formed only in certain places, though the future outline of the canals is descernible, as a well marked epithelial thickening, indicated, in figs. 28 and 29, by a dotted line. A feature characteristic of this fish, as well of *Moxostoma*, is the large number of neuromasts in the canals.

The supraorbital canal is closed only in its middle frontal part, which contains five neuromasts. Rostrally and caudally, the area of the future canal is visible. Thus, rostrally, the nasal portion extends to the level of the anterior nasal opening. This part contains three organs. In connection with these organs three separate nasal bones have already begun to form. Caudally to the canal the epithelial thickening continues over the frontal bone and further on the anterior half of the parietal bone. The frontal portion lodges four organs, the parietal two. All in all, fifteen nueromasts will appear in the fully developed supraorbital canal. As previously stated, with regard to *Abramis*, the n. opht. sup. V and VII are separate, leaving the cranium each through a foramen of its own, uniting just after the passage. Proximally, an intracranial branch issues from the ophthalmic nerve VII. This branch soon after bifurcates. One of the branches immediately passes through a foramen in the cranium,

proceeding to organs in the temporal canal, i.e. the n. oticus. The other branch continues intracranially to the dorsal side where it pierces through the parietal bone. Outside this it divides, innervating four neuromasts in the prolonged supraorbital line, two of which being situated on the frontal, two on the parietal bone. Furthermore, from the n. opht. VII an additional branch issues which, after having passed through the frontal bone, innervates the two hindmost canal neuromasts, as well as one, or, possibly, two organs in the prolonged portion. All other organs in the line are innervated by extracranial branches. Apart from these canal neuromasts, a great many free organs are innervated by this nerve. Also in this fish, the previously described lines will be observed. Rostrally, a short nasal pit-line (*na.l.*) bends laterad rostrally to the anterior nasal opening, as a continuation of the nasal canal. In addition, a markedly developed medial supraorbital line (*m.so.l.*) appears, which, on a level with the nasal openings, meets the corresponding line from the opposite side, thus forming a pit-commissure. Likewise, laterally to the canal, a well developed lateral line (*l.so.l.*) bends downwards behind the eye.

The future outline of the infraorbital canal (*io.l.*) is represented only by the epithelial thickening. The canal has developed merely in the antorbital region. There two independent canal portions appear, each containing one neuromast. The fully developed canal will probably contain twentyfour neuromasts, viz. seven in the antorbital bone, six in the first and seven in the second infraorbital bone. Whether the four remaining neuromasts will lie in a third similar bone, is, though likely, impossible to ascertain from the material at my disposal. There is an accessory infraorbital line parallel with these organs. In this fish this line is divided into two parallel lines, one close to the canal organs, the other lying at some distance ventrally to it. Further, the n. buccalis VII innervates a well developed rostral pit-commissure, as well as an antorbital line.

In the mandibulo-preopercular line only the middle part of the preopercular canal (*po.c.*) is invaginated. At the mandibular joint there is an interruption in the thickening. According to ANDRES (1899) and ALLIS (1904), this fish should be without a mandibular canal. However, an examination of old specimens has shown that such a canal, well developed, exists, extending towards the anterior end of the mandible. Dorsally to the upper portion of the preopercular canal a pit-line of six organs is to be noted. At this stage, an epithelial thickening appears between these organs. In full-grown specimens the canal reaches considerably farther up towards the temporal canal than at this stage. Also these organs are thus, likely to form part of the canal, though they will sink in much later. Altogether, about thirty organs will probably be included in the mandibulo-preopercular canal, ten in the mandibular portion and the remaining ones in the preopercular. All are innervated by the external

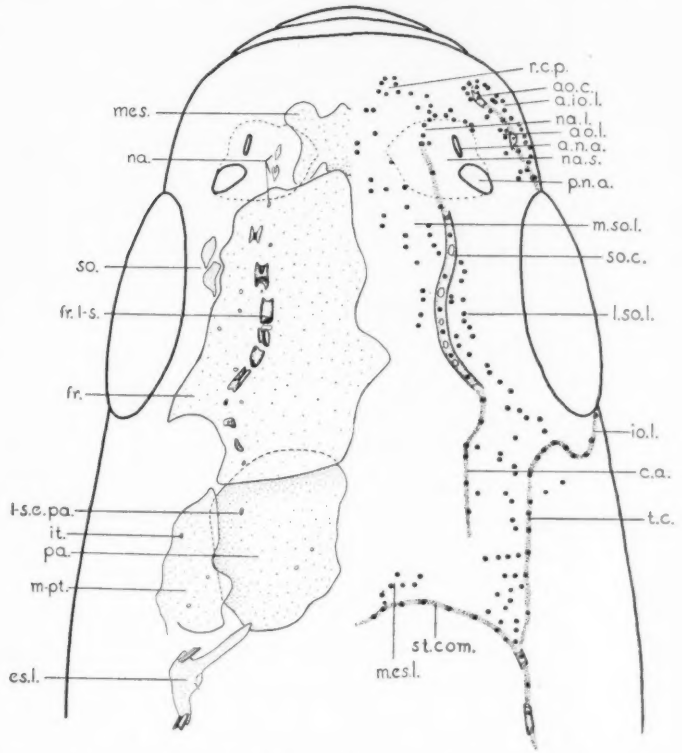

Fig. 29. *Tinca tinca*, 46 mm. Head from dorsal side. Bones on left side, lateral line system on right side. 11 ×.

mandibular nerve, with the exception of the six uppermost organs, which are innervated by branches of the opercular nerve.

The lines on the cheek are particularly well developed. The horizontal pit-field, i.e. the vertical pit-line, is in this place divided into a number of lines that present a striking similarity to the corresponding lines in the Gobiids. In, e.g., *Gobius niger* (SANZO 1911 and own unpublished investigations), the nerve to the vertical line innervates a horizontal line below the eye, which is divided into an anterior and a posterior part, as well as a line parallel with the preopercular canal and, finally, a corresponding line parallel with the mandibular organs. Fundamentally, the same distribution of the lines is to be found in *Tinca*. Thus, there are a line parallel with the mandibulo-preopercular line (the canal), a horizontal line, divided into an anterior and a posterior portion, and, in addition, a line parallel with the mandibular line. The horizontal pit-line here appears as a vertical line immediately in front of, and parallel with, the upper part of the preopercular canal.

The opercular lines conform to those in the previously analysed fishes. Thus, a well developed vertical and a lower horizontal line, as well as a more irregular upper horizontal line appear.

The temporal canal contains nine organs. The four first and the two last ones are innervated by the otic and the glossopharyngeal nerves, respectively. In the three intermediate organ I have, unfortunately, been unable to ascertain the innervation. In addition, the otic nerve innervates a number of free neuromasts between the temporal canal and the "canal antérieur". Likewise, a number of organs dorsally to the canal are innervated by the glossopharyngeal nerve. The supratemporal commissure lodges seven organs innervated by the vagus. Immediately rostrally to the supratemporal commissure lies the medial extrascapular line. Finally, the main canal of the body has, partly, begun to sink in. Also here, independent portions of the canal form round each neuromast. These canals later fuse with one another.

7. THE LATERAL LINE SYSTEM IN *NEMACHILUS BARBATULA* L.

(Figs. 30—37.)

Data concerning the lateral line system in the Cobitids are extremely sparse in the literature. MIYADI (1929), gave a summary description of the canal system in some Japanese species, arriving at the conclusion that the canal system in the Cobitids must have been reduced or be involved in a process of reduction. He has found a considerable inconstancy with regard to the pattern and development of the canals. The same system would sometimes differ from the right side to the left in the same specimen. In his work on the function of the lateral line system, DYKGRAAF (1934), includes a general picture of the position of the sense organs in this species. The picture is, however, extremely schematic, and the description does not enter into any details.

In several respects, the lateral line system in this fish differs from the previously described species, both with regard to formation, development and pattern. Nevertheless, the fully developed system well fits in with the general scheme of the Cyprinids.

At the *3.4 mm stage* (fig. 30), the lateral line system is already well developed. Unlike the earlier stages of *Leuciscus* and *Phoxinus*, a number of pit-lines are formed, a matter of particular interest, considering that the development of these lines can be followed from an early stage up to the adult. The horizontal and vertical pit-lines are of special interest. In the above-mentioned fishes these lines will appear comparatively late, in *Leuciscus* at the 14 mm stage, and have the same position and extent as in adult specimens.

The supraorbital line (*so.l.*) lodges four organs, the two foremost ones lying behind the nasal placode, on a level with the anterior edge of the eye. They afterwards become the two foremost organs in the frontal canal. The following

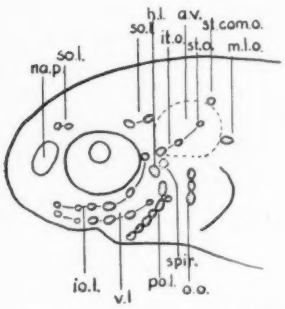

Fig. 30. *Nemachilus barbatula*, 3.4 mm. Lateral line system of head. 50 ×.

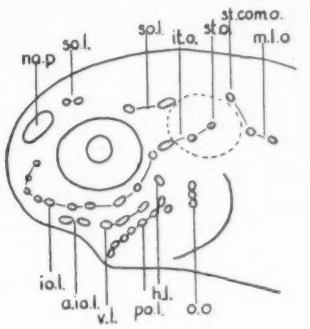

Fig. 31. *Nemachilus barbatula*, 4.0 mm. Lateral line system of head. 60 ×.

organs are situated on a level with the posterior edge of the eye and the anterior part of the auditory vesicle. All the organs will, in due course, lie on the future frontal bone. The hindmost organ is homologous with that or those organs in the Cyprinids that are to form part of the prolonged supraorbital canal (the "canal antérieur") and to lie either on the frontal or the parietal bone. This species does not show any marked prolongation of this canal. It is obvious, however, that the hindmost portion of the canal corresponds to the prolonged canal in the other species.

The infraorbital line (*io.l.*) consists of six organs lying in a curve below the eye, with the foremost organ approximately on a level with the anterior edge of the eye. Behind the eye the line passes directly into the temporal line. Already at this stage it is possible to distinguish between the two organs innervated by the otic nerve and the glossopharyngeal organ. Also in this fish they occupy the same position in relation to each other as in the previously described species.

The lines on the cheek are well developed. One of these lines extends in an even curve from the hindmost (uppermost) infraorbital organ across the cheek down towards the mandibular symphysis. It will be seen from later stages that this seemingly single line consists of several components. The uppermost organ will form part of or, possibly, originate the horizontal pit-line. The lower organs will be found in the oral pit-line, while the medial ones will form the mandibulo-preopercular and the accessory preopercular lines.

A horizontal line of six organs extends backwards to the above described line parallel to the infraorbital line. Also this line is made up of components. As will be found later, the foremost organs are innervated by the buccal nerve. They, thus, belong to the infraorbital line and may be said to constitute the accessory infraorbital line. The hindmost organs, on the other hand, have another innervation, and form the vertical pit-line (*v.l.*).

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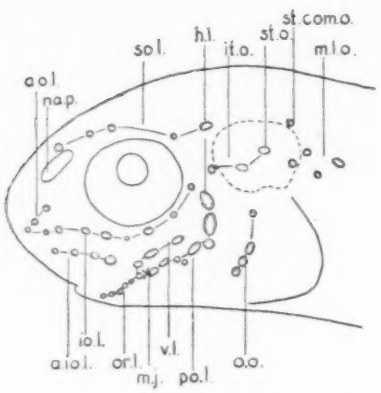

Fig. 32. *Nemachilus barbatula*, 4.3 mm. Lateral line system of head. 60 ×.

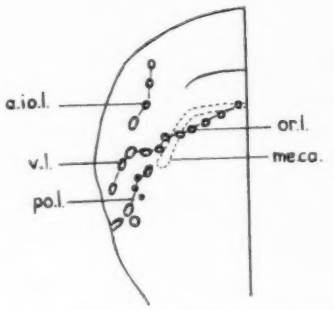

Fig. 33. *Nemachilus barbatula*, 4.3 mm. Lateral line system from ventral side. 60 ×.

On the gill-cover a vertical opercular line of three organs is to be noted. As to the organs innervated by the vagus, one is found dorsally to the auditory vesicle (*st.com.o.*), to be included later in the supratemporal commissure, another behind the vesicle, later to form part of the main canal of the body (*m.l.o.*).

At the *4.0 mm stage* (fig. 31), the same lines as before are to be seen, while many other organs have been added. Thus, the infraorbital line has grown rostrad, now bending upwards in front of the eye. The other lines remain comparatively unchanged. In the horizontal line below the infraorbital line, an anterior and a posterior portion with two and three organs, respectively, can be discerned.

At the *4.3 mm stage* (figs. 32, 33), a further number of organs have appeared, while the lines have begun to change their course. In the supraorbital line a nasal organ has been added medially to the nasal placode. In the infraorbital line a change is to be noted, in so far as the foremost organs do no longer constitute an even curve but an acute angle. At this stage the organs on the cheek have begun to arrange themselves into their definitive lines. From the hindmost infraorbital organ down towards the mandibular joint, a semicircular line extends containing the horizontal pit-line organ (the uppermost organ, *h.l.*), as well as the organs of the preopercular line. Here these organs lie somewhat irregularly, owing to the fact that they have begun to arrange themselves partly in an accessory, partly in a properly preopercular line. Immediately in front of the mandibular joint (*m.j.*), the vertical pit-line (*v.l.*) obtains a continuation in the oral line which extends down towards the mandibular symphysis where it meets the corresponding line from the other side. This connection has not been clearly manifest at the earlier stages, but here, especially in the reconstruction from the vertical side (fig. 33) it is

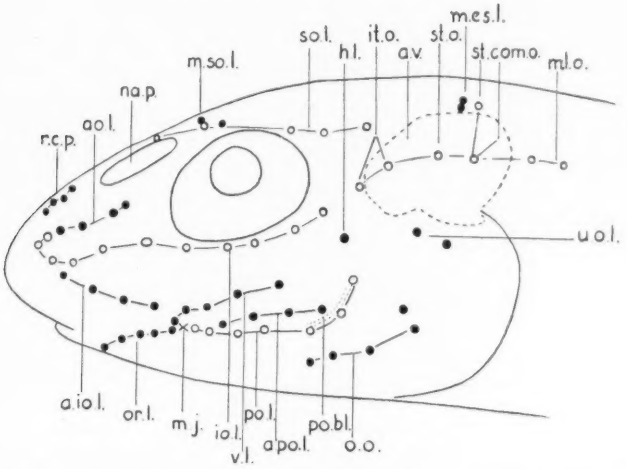

Fig. 34. *Nemachilus barbatula*, 5.3 mm. Lateral line system of head. Black dots—organs in pit-lines. Rings—organs in future canals. 17 ×.

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distinctly visible. Here the horizontal line (*a.io.l.*) innervated by the buccal nerve consists of four organs, probably originating from a division of the two previous ones. As regards the other organs, a vertical line on the gill-cover has now assumed a somewhat oblique direction. On the gill-cover an additional organ has appeared, probably belonging to the upper horizontal line.

At the *5.3 mm stage* (fig. 34), the fish has reached such a development as to give the lines roughly the same extent as in an adult specimen. In the supraorbital line some new organs have appeared. As yet, only one nasal organ is found, but four frontal ones. Medially to the foremost of these, an organ has appeared which will in time form part of the medial supraorbital line (*m.so.l.*). On account of the marked growth of the nasal portion, the anterior part of the infraorbital line has been stretched longitudinally and, because of this, the part of the line that was previously directed upwards has become more or less parallel with the rest of the line. The four hindmost organs in the upper branch constitute the antorbital line (*ao.l.*), while the remaining part will become canal neuromasts. Dorsally to the upper portion of this line a number of organs has appeared, the rostral pit-commissure. The preopercular line (*po.l.*) consists of seven organs. Beneath the three hindmost of these organs a preopercular blastema has begun to form (*po.bl.*). Between the hindmost of these organs and the last infraorbital organ a solitary organ is still to be seen, which will later become the horizontal pit-line. Side by side with the preopercular line a distinct accessory line (*a.po.l.*) has developed. The vertical pit-line is, also at this stage, connected with the oral line at the mandibular joint. On the gill-cover, the previously vertically arranged organs have considerably changed

their interrelationship. Now they form a practically horizontal line. This change is due to the pronounced movement forwards of the mandible. In the course of this process the line has migrated forwards to such an extent as to place the undermost (foremost) organ below the preopercular line. The originally vertical line has obtained its definitive outline, having been transformed into a lower horizontal opercular line. Yet another organ has appeared in the upper horizontal opercular line. The same has happened in the definitive vertical line.

The forementioned deviation has, probably, also influenced the temporal line in which the organ innervated by the glossopharyngeal nerve has moved downwards, thus assuming a position more in line with the otic organs. In addition, two neuromasts have appeared, rostrally to the organs of the supratemporal commissure, constituting a beginning of the medial extrascapular line.

During the next stages many free organs will be added, in connection with such lines as already exist. Since their innervation is difficult to ascertain at such young stages, an identification of the different lines becomes almost impossible, especially on the cheek. For this reaon, I shall proceed directly to far more advanced stages, where the innervation is easier to trace and the canals have begun to form.

A first indication of the formation of the canals is revealed when the fish has reached a length of 20 mm. Then the antorbital part of the infraorbital canal begins to sink in. At the 21 mm stage, this portion of the canal has closed. At the 26 mm stage (fig. 35) these processes in the canal have reached to the level of the anterior edge of the eye. The canal is being formed in the shape of independent segments that soon will fuse into one. At the same stage, also the main canal of the body has formed. It begins to sink in on a level with the gill-cover, then continuing forwards and backwards on the body.

At the *33 mm stage* (fig. 36), the infraorbital, temporal and vagus-innervated canals have sunk in in their entirety. No hint of the other canals is as yet to be discovered. It should be noticed that the fundamental difference between this fish and previously described Cyprinids is evident already at this period. In the latter the supraorbital and mandibulo-preopercular canals are formed far earlier than the infraorbital canal which, even in a late phase of development, still remains incomplete. Thus, in this fish the course is exactly the reverse.

At this stage (33 mm) the infraorbital canal is wholly formed. Rostrally, it bends sharply towards the dorsal side terminating in a pore on the dorsolateral side of the nose. This upward part lodges one neuromast. The next pore is directed straight forwards. Altogether, the canal contains eleven organs innervated by the buccal nerve. As in the previously examined species, the first organ in the canal is innervated by an independent branch, issuing from the buccal nerve on a level with the anterior edge of the eye. Unlike the forementioned fishes, in *Nemachilus* this canal passes caudally directly into the temporal canal. This latter canal comprises the normal number of two organs

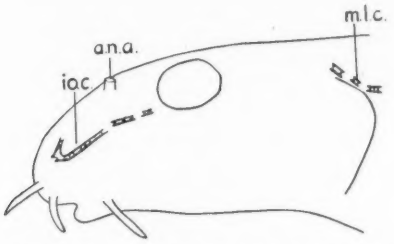

Fig. 35. *Nemachilus barbatula*, 26 mm. Canals of head and anterior part of body. 10 ×.

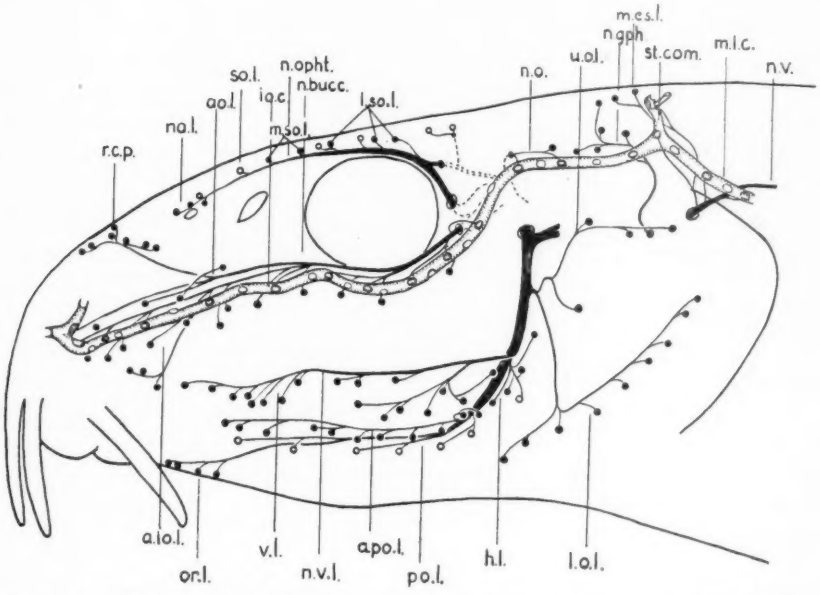

Fig. 36. *Nemachilus barbatula*, 33 mm. Lateral line system of head. Black dots—organs in pit-lines. Rings—organs in future canals. 17 ×.

innervated by the otic nerve and one by the glossopharyngeus. This canal in its turn passes directly into the supratemporal commissure and the main canal of the body. The other canals have not as yet been formed. But, below the organs that later will become canal neuromasts, canal bones have, at this stage, begun to form. Because of this fact, these neuromasts can be distinguished from the free organs. In the figure, these future neuromasts have been designated by a ring, while the free organs are indicated by a black dot.

The supraorbital line does not reach the rostral commissure. The line consists of six future canal neuromasts. The two anterior will, in due course, be found each in a nasal bone of its own, while the four posterior ones will lie in the frontal bone. Further, a few free organs are to be noted. Rostrally and

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laterally to the anterior nasal organ, three organs are observed (*na.l.*), corresponding to the nasal pit-line in the previously described fishes. Then, two organs appear medially to the canal (*m.so.l.*), representing the medial supraorbital line and, finally, three organs laterally to the canal organs, corresponding to the lateral supraorbital line (*l.so.l.*). In contrast with the observations in the fishes previously dealt with, these lines are here but very faintly developed. In this fish the n. opht. V and VII issue from different foramina, uniting after a short passage. All the organs, apart from the two hindmost, are innervated by extracranial branches of the superficial ophthalmic nerve, the two hindmost being innervated by one common branch, issuing from the intracranial part of the n. opht. VII. On the other hand, no nerve issues together with the n. oticus. In the before analysed fishes the organs that form part of the prolonged supraorbital canal are innervated by intracranial branches. This fish does not possess any conspicuously long canal, though the innervation and the embryology of the organs suggest that they are homologous with those of the prolonged canal.

Also here a number of lines occur in connection with the infraorbital canal. Immediately ventrally to the entire canal, a row of neuromasts appear, constituting an accessory infraorbital line (*a.io.l.*). Dorsally to the anterior part of the canal, a line of four organs lies parallel to the canal. These organs are innervated by the same lateral branch that proceeds to the first canal neuromast and the rostral pit-commissure. This line (*ao.l.*) is homologous with the antorbital line in the previously described fishes which, in them, extends from the anterior part of the canal obliquely up backwards between the posterior nasal opening and the eye. At the 5.3 mm stage this line disclosed a similar extension but, in the course of the development, the nasal portion grows markedly in length, particularly because of the development of the accessory nasal cartilages. Owing to this process also the pit-line moves forwards, thus finally obtaining the forementioned course.

At this stage the mandibulo-preopercular line can be easily distinguished, since canal bones have begun to form below the neuromasts. The line is composed of seven organs, the two foremost situated in the angular-splenial bone and the remaining ones in the preoperculum. A mandibular line in the proper sense is missing. Thus, as will be shown later, no dental-splenial bones are to be found. On the other hand, ventrally to the mandible a short pit-line is to be seen. At the 5.3 mm stage it was connected with the anterior part of the vertical pit-line. Here it has freed itself from this connection. Dorsally to, and side by side with, the preopercular organs, a well developed accessory preopercular line (*a.po.l.*) is to be noted.

Here, the vertical pit-line (*v.l.*) is observed in a position wholly differing from that of the earlier stages. Because of the general changes of position, caused by the growth of the mandible, as mentioned above in relation to the

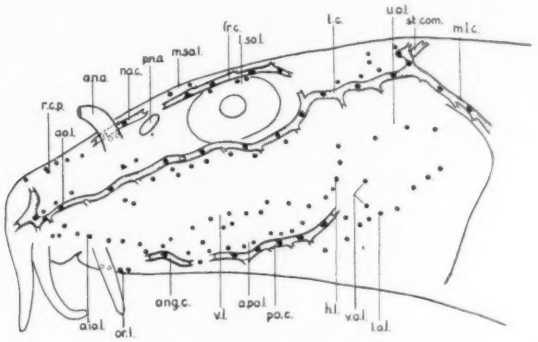

Fig. 37. *Nemachilus barbatula*, 70 mm. Lateral line system of head. 6 ×.

opercular organs, also this line has moved forwards, thus assuming a horizontal position. The same applies to the horizontal line (*h.l.*), which has now a vertical direction, and is to be found immediately in front of the hindmost preopercular organ. The innervation of the last-mentioned lines agrees entirely with that of the previously examined fishes. Mention should, however, be made of the fact that the nerve to the vertical line leaves the T. hyoideo-mandibularis within the hyomandibular bone, passing that bone through a foramen of its own. It does not penetrate the musculus adductor mandibulae, as in previously analysed fishes, but proceeds directly out into the skin behind this muscle.

On the gill-cover the three usual lines are to be found, viz. a well developed lower horizontal line and a faintly developed vertical and upper horizontal line.

The position of the free organs innervated by the n. glossopharyngeus resembles that of the corresponding organs in the fishes referred to above. However, in this particular species an organ has moved far up towards the dorsal side, and this organ may, possibly, correspond to a middle pit-line. Just in front of the supratemporal commissure a medial extrascapular line with two organs will be found.

At somewhat older stages the other canals begin to sink in. Thus, all the canals are fully developed in a 47 mm long specimen. The appearance of the full-grown animal will be seen from fig. 37. The infraorbital canal and its continuation present the same aspect as before, though the pore-tubes have lengthened. The supraorbital canal consists of two independent canals, viz. a nasal part with two organs, and a frontal part with four organs. In this specimen, the mandibulo-preopercular canal is likewise composed of two canals, viz. an angular and a preopercular part with one and five organs, respectively. Between the canals, an organ belonging to the angular part is to be seen. In other specimens the two canals may be connected. In certain canals the number

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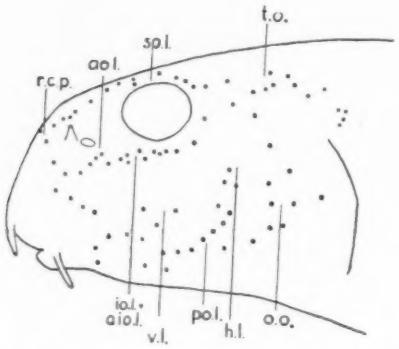

Fig. 38. *Cobitis taenia*, 70 mm. Lateral line system of head. 5 ×.

of neuromasts may vary rather considerably from one specimen to another. Even in the same specimen the number may differ from the left to the right side. Thus, in the frontal canal the number varies between four and five, and in the infraorbital canal between nine and thirteen.

Roughly, the pit-lines offer the same appearance as at the 33 mm stage. However, in the present specimen the horizontal pit-line lies somewhat farther towards the dorsal side.

8. THE LATERAL LINE SYSTEM IN *COBITIS TAENIA* L.

Nor in this instance has, to my knowledge, any description of the lateral line system been published. I have had at my disposal a number of full-grown specimens. No embryos have been available.

In this fish the lateral line system differs from all those previously examined, in so far as canals are missing even in the full-grown animals. The lateral line system consists of nothing but a number of free neuromasts. Their position will be seen from fig. 38. Fundamentally, the pattern conforms to that in *Nemachilus barbatula*. Inter alia, mention should be made of the fact that the infraorbital line continues directly into the rostral commissure. Also, a short antorbital line is to be found, as well as an anterior horizontal line innervated by the buccal nerve. An horizontal line (*v.l.*) on the cheek, innervated by the nerve to the vertical line is but faintly developed, consisting of some few organs only.

In this connection it should be observed that, according to MIYADI (1929), canals are to be noticed only in the anterior part of the body of *Misgurnus anguillicaudatus*, and that the same applies to *Cobitis biwae* and *Misgurnus decemcirrosus*. In *Lefua echigonia* canals are entirely missing.

9. THE LATERAL LINE SYSTEM IN THE SILURIDAE.

The canal system in these fishes has been subjected to a number of investigations. Mention should be made of POLLARD (1882), HERRICK (1899, 1900, 1901), ALLIS (1904), FRIEDRICH-FREKSA (1930), among others. Generally, the canals offer but little interest. Fundamentally, they do not differ from the Cyprinids. Some differences should, however, be stated. In the Silurids the canals often open into long pore-tubes that, occasionally, may form commissures with one another. This applies, e.g., to the supraorbital canals, which, in *Clarias, Chaetostomus* (POLLARD) and *Plotosus* (FREKSA) are mutually connected by a pore-tube commissure. In the last-mentioned fish the pore-tubes are, in addition, markedly ramified, in the same way as in *Amia*. Generally, the canal system is better developed in the Silurids than in the Cyprinids. Thus, the infra- and supraorbital canals are connected behind the eye. Also, as a rule, the preopercular canal opens in the temporal canal. On the other hand, a fully developed supratemporal commissure seems to be missing. As in the previously described fishes the supraorbital canal is, as a rule, prolonged, though not to the same extent. It contains but one organ and most frequently continues in an anterior head pit-line. The prolonged canal of the Silurids corresponds only to the anterior part of the corresponding canal in *Leuciscus*. The neuromasts are otherwise, in every case, comparatively few. Thus, in the temporal canal only two organs, one innervated by the n. oticus, the other by the n. glossopharyngeus, are to be noted. As to the time of the formation of the canal I have found only one statement. According to HERRICK (1899), there are no canals to be found in an 1 cm long *Menidia*. In specimens a few millimetres longer the canals had begun to form and, in a 2.5 cm long specimen, they had assumed largely the same appearance as in an adult. As compared to the previously examined fishes the canals appear extremely early. Also other facts suggest that this is, apparently, normal.

The pit-lines are, in comparison with the above analysed fishes, extremely few and faintly developed. Unfortunately, but a few Silurids have been examined in this respect, to my knowledge only *Menidia* (HERRICK 1899), *Amiurus* (HERRICK 1901) and *Silurus* (ALLIS 1904).

Thus, according to ALLIS, there are in *Silurus*, on the dorsal side, a short rostral pit-commissure and an anterior and a middle head pit-line, and, on the cheek two lines, probably identical with the vertical and horizontal lines. Since the innervation is unknown, the interpretation cannot be quite definite. In *Amiurus* the following lines are distinguishable: on the dorsal side a rostral pit-commissure, an anterior, a middle and possibly a posterior head pit-line and a line along the preopercular canal, innervated by the n. mandibularis externus. In *Menidia* the following lines are observed: a line of four organs, at the ventral edge of the operculum, and two organs, at the dorsal edge of the same

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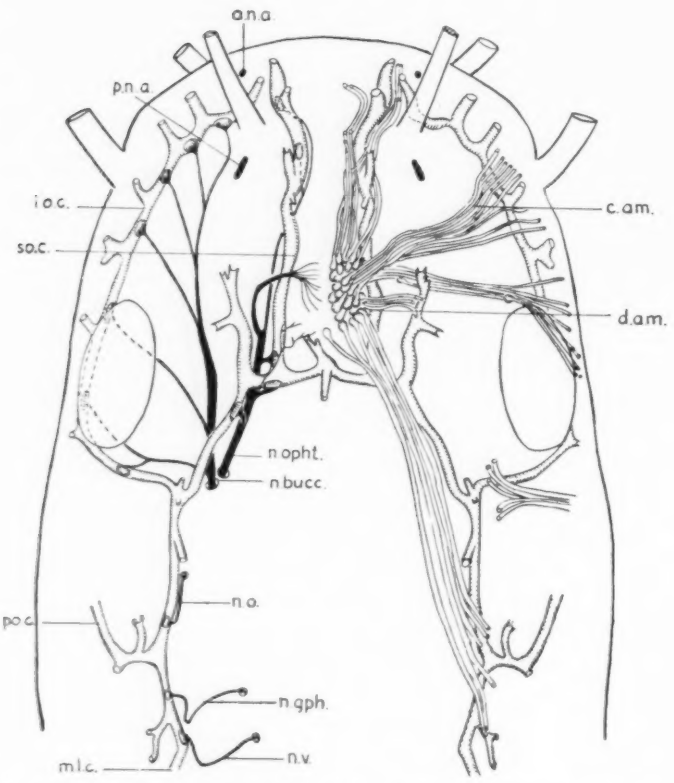

Fig. 39. *Plotosus anguillaris*, 43 mm. Lateral line system. Nerves on left side, ampullae and canals of Lorenzini on right side. 13 ×.

bone. One organ lies in front of the vertical part of the preopercular canal. Along the horizontal part of the same canal a line is noticed, and a similar one occurs along the mandibular canal. In addition, medially to the anterior end of the last-mentioned canal, an organ forms with its vis-à-vis "a mandibular commissural line". Further, a rostral commissure and some organs round the anterior nasal opening are to be noted. From this it is evident that the line system of at least these forementioned Silurids is very weakly developed, as compared to the previously analysed fishes.

Plotosus anguillaris, whose peculiar lateral line system was described by FRIEDRICH-FREKSA in 1930, is, indubitably, among the most interesting Silurids in this connection. Apart from a normal canal system, this fish has a great number of ampullae of Lorenzini, a feature, which, according to present knowledge, is unique among Teleosts. The investigation by FREKSA, which is, partly, anatomical, and, partly, histologic, dwells chiefly on the histology of the ampullae, the conclusion being that they are homologous with the corresponding

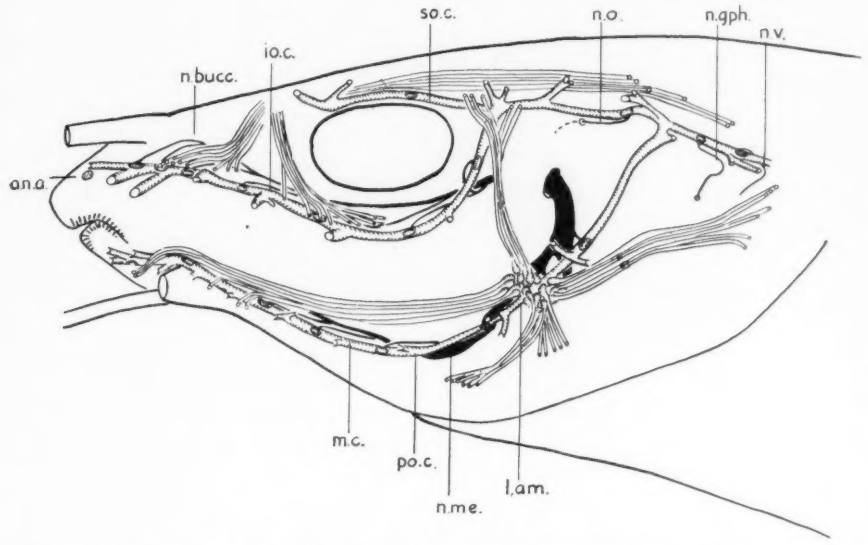

Fig. 40. *Plotosus anguillaris*, 43 mm. Lateral line system with ampullae and canals of Lorenzini. 13 ×.

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organs in Selachians. While in the last-mentioned fishes the ampullar duct medially divides into several ampullae, the only difference seems to be that, here, the duct is simple, each ampulla being provided with a duct of its own. Since FREKSA's pictures of the courses and the interrelationship of the canals and the ampullar ducts are extremely schematic, I have examined the same fish. For this purpose, I have had at my disposal a number of 40—45 mm long specimens from the Seychelle Islands. A specimen, 43 mm long, has been sectioned and reconstructed (fig. 39, 40), with a view to analysing the interrelationship of the canals, the ampullar ducts and the innervation of the sense organs. The canals do not offer much of particular interest. As a rule, they open into long pore-tubes which, in older specimens, may be considerably ramified. At this stage, the pores are mostly simple, but a few having begun to divide. As mentioned above, a supraorbital tube-commissure is to be noted between the eyes. The innervation of the canal organs is entirely normal, as will be seen from the figures. The most interesting feature is without doubt the ampullar system. As demonstrated by FREKSA, these ampullae are assembled within three areas in the head, viz. one single on the dorsal side between the eyes, the other two situated one on each cheek. From these ampullar fields the ampullar canals radiate, opening into fine pores in the epidermis. From the dorsal field they spread in ten directions. One group proceeds rostrad, opening round the anterior part of the supraorbital canal. Clockwise, the next group will open out on a level with the anterior part of

the infraorbital canal, and the following one at the same canal below the eye. As far as this lastmentioned group is concerned, FREKSA has made a mistake, in so far as he has drawn the ampullar canals that open out here down to the lateral ampullar field. The last group but one opens out on the dorsal side, at the long tube that issues from the supraorbital canal. Finally, through extremely long canals on the dorsal side, the last group opens out on a level with the connection between the preopercular canal and the temporal canal.

The canals radiate from the lateral ampullar field in five directions, viz. three on the gill-cover, one along the mandibular canal, and one on the dorsolateral side, at the place where the infra- and supraorbital canals meet.

It is obvious from the interrelationship of the canals and the ampullar ducts that the latter must originate earlier than the former, since, in several places, the ampullar ducts lie laterally to the canals. According to FREKSA, the ampullar system develops as follows: to begin with the ampullar organs lie in the epidermis, then they sink in and meet in the above-mentioned fields. My observations agree in this respect with FREKSA's. In the specimen examined by me some ampullae have as yet failed to reach their destination, and have only traversed a short distance of their inward migration. Thus, one ampulla is seen immediately in front of the eye. In other words, the primary position of the ampullar organs must be the place where the canals open into the epidermis.

The innervation of these ampullae is easy to ascertain but, nevertheless, it remains a riddle. The dorsal field is innervated by the n. opht. VII and the lateral fields by the n. mand. ext. Supposing, as suggested above, that the ampullar organs have originally been situated at the mouths of the canals and that a migration inwards has later taken place, also the nerves must have been involved in this migration. That they have, in all probability, partly done so is evident from the fact that, e.g., the nerve branches to the dorsal ampullar field run dorsally to the canal. However, also the nerve must, to begin with, have extended to the original position of the organ. An examination of early embryonic stages is a necessary prerequisite, if an attempt is to be made to decide, from available facts, how the dorso-caudal ampullar group happened to be innervated by such a short nerve branch. A different innervation should have been expected, considering the original position of the organs. The organs along the infraorbital canal should have been innervated by the buccal nerve, while the posterior dorsal group should have been innervated by the glossopharyngeal or vagal nerves. No such innervation has proved ascertainable in the examined specimen. This matter will be further referred to in the general discussion.

This fish has a great many terminal buds in the epidermis, while totally lacking free neuromasts.

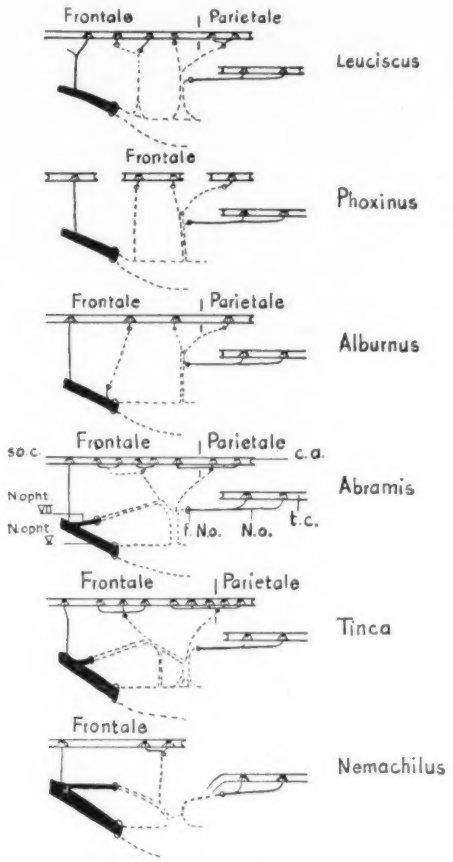

Fig. 41. Diagram of innervation of the posterior part of the supraorbital and anterior part of temporal canals.

IV. THE CANAL BONES.

As stated in the introductory remarks, only a few Teleosts have been subjected to any minute analyses with regard to the formation and development of the canal bones. Most attention has been paid to *Esox*, by PEHRSON (1944 a), and to certain species of *Salmo*, by DEVILLERS (1944 a, b, 1947). For the purpose of certain comparisons the latter also examined *Leuciscus*. Better known are the Ganoids, from investigations, inter alia, by PEHRSON of *Amia* (1922, 1940), of *Polyodon* and *Acipenser* (1944 b) and by HAMMARBERG of *Lepidosteus* (1937).

Considering that such a limited number of Teleosts have been examined, and, further, that the formation and development of the bones, as will be shown

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below, vary more than there was reason to suppose previously, I shall not propose to submit any general interpretation of the formation and development of these bones but chiefly concentrate upon the Cyprinids and Cobitids. Unfortunately, I have not had access to suitable material of any Silurid. For this reason, the latter family has for the present had to be disregarded.

In the following account of the formation and development of the bones, particular attention has been directed to the mutual relationship between the membranous and latero-sensory components. For this reason, the examined fishes have been described in the following order: first, a species where the two components are united from the beginning, then species where these two parts gradually become independent of each other.

1. THE CANAL BONES IN *LEUCISCUS RUTILUS* L.

(Figs. 12, 42—46.)

Bones formed in connection with the supraorbital canal.

As in other Teleosts, two bones, viz. the nasal and the frontal, are formed in connection with this canal but, in addition, in this fish latero-sensory elements connected with the prolonged supraorbital canal appear.

The nasal bone. The first primordium of this bone is to be seen in a 20 mm long specimen as a single blastema below the hindmost of the three nasal organs. The sense organs still remain in the epidermis, and no indication that the canal is about to sink in can be noticed. At the 22 mm stage bone elements have formed in the blastema. Thus, a thin, slightly furrow-shaped bone extends below the two hindmost organs. Whether the bone has formed in two places, or whether it has appeared as a unity from the beginning, cannot be decided here. At the 26 mm stage the canal begins to sink in. The bone is in a transverse section, semicircular. It has grown still more forwards, reaching with its anterior part to the first nasal organ. At the 44 mm stage (fig. 42), the two nasal bones differ from one another, owing to an abnormality in the development of this specimen. At one side, the canal has sunk in quite normally and, here, the nasal bone consists of a tube-shaped bone containing two neuromasts. No lamellae are to be found on the bone. On the other side of the head, the canal has not sunk in, and the organs still remain in the epidermis. Here, the nasal bone consists of two independent bone lamellae. True, two organs lie above the anterior bone, but they have, in all likelihood, arisen through a secondary division of one organ. Above the posterior bone one sense organ is to be found. This may indicate that the nasal bone originates in two originally independent bones that in time fuse into one unified tube-shaped nasal bone. As will be shown later, this is usual in the analysed species.

The frontal bone. In contrast with the nasal bone, this bone is formed by

Fig. 42. *Leuciscus rutilus*, 44 mm. Nasals. 13 ×.

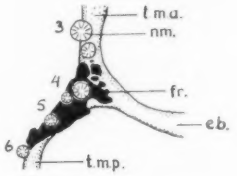

Fig. 43. *Leuciscus rutilus*, 9 mm. Left frontal bone with parts of taeniae marginales. 60 ×.

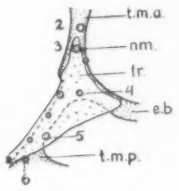

Fig. 44. *Leuciscus rutilus*, 9.5 mm. Left frontal bone with parts of taeniae marginales. 40 ×.

stages, viz. first a lamellar part, the "composant membrano", acc. DEVILLERS (1947), and, much later, a latero-sensory component, the "composant dermo". Unlike most other here examined fishes, the latero-sensory component is, from the beginning, more or less closely united with the membranous one.

The first primordium of the membranous component appears, when the fish has attained a length of about 9 mm. The bone rudiment, at this stage, consists of a considerable number of strips of bone pieces of an irregular shape. Fig. 43 gives an idea of their general appearance. They appear to be the result of an ordinary membranous ossification. As will be seen from the figure, the first primordium of the bone is noticed chiefly on the taenia marginalis posterior, in connection with the organs 4 and 5. Further, a fine strip of bone extends up above the epiphysial bridge.

In a specimen, only slightly older, 9.5 mm, fig. 44, the bone has already grown considerably, now covering the whole of the taenia marginalis posterior and the greater part of the epiphysial bridge. The frontal bone is now a single bone, since all minor independent ossifications have fused into one. Any attempt to homologize the neuromasts that appear between the two reproduced stages must become uncertain, in view of the appearance of some new ones, belonging to the lateral and medial supraorbital line. The fully developed frontal bone lodges six neuromasts (fig. 12). An endeavour has been made to identify these neuromasts in fig. 43, but the results are not reliable. In such an instance, the frontal bone would, at the 9 mm stage, be connected with the organs 4 and 5. At an older stage, the bone lies below the organs 3—6, practically extending to the organ 2. A comparison between the two stages shows that the bone chiefly grows forwards and medially to the epiphysial bridge. No active participation of the sense organs in the ossification has been ascertained.

The next stage in the formation of the frontal bone occurs only when the supraorbital canal begins to sink in, viz. at the 18 mm stage. Already in a 16 mm long specimen, the blastemas have begun to form, in connection with the primary neuromasts. Thus, a blastema extends from the edge of the

neuromasts obliquely down towards the underlying membranous part of the frontal bone. In an 18 mm long specimen ossification has begun in this blastema. This ossification always sets in where the blastema adjoins to the membranous part, thus causing an impression that the latero-sensory component grows out from the membranous one. However, in certain places the first ossification can be seen to take place independently of the membranous component, though the two components will very soon fuse with one another. In other analysed Cyprinids the latero-sensory part ossifies quite independently and will fuse with the membranous part far later, or the two parts may remain mutually independent throughout life. From this it will be evident that also in *Leuciscus* two components are concerned, though they are already from the beginning united or will very soon fuse with one another. As the canal sinks in, the latero-sensory component gradually grows, having, when the canal has closed, entirely surrounded it. In a 26 mm long specimen the canals are completely formed and closed round the four first organs in the frontal canal, but beneath the four other organs no ossification has as yet set in. The latter bones, that lie round the "canal antérieur", form extremely late, as compared to the properly frontal latero-sensory elements. As previously shown, the posterior part of this canal lies on the parietal bone. Also round this part a latero-sensory component will develop, closely fused with the underlying parietal bone. However, the anterior part of this component invariably remains independent (fig. 46). I shall return in a later connection to an interpretation of this component of the parietal bone.

As far as the frontal bone of this fish is concerned, DEVILLERS (1944 a, p. 29) has come to the same conclusion regarding the development. He says as follows: "Pour le frontal — — — je n'ai pas rencontré de blastème juxta-épithélial. Ces os se développent au milieu du conjonctif comme des os dermiques ordinaires (parasphénoïde, opercule) et toute leur morphogenèse s'accomplit en contact étroit avec les cartilages craniens. Les composants dermo, par contre, n'ont pas évolué, et au niveau de chacun des organes on trouve toujours deux ailes, d'abord indépendantes puis soudées au membrano."

Bones formed in connection with the infraorbital canal.

As in the case of the other examined Cyprinids, a large antorbital bone, and behind it usually three infraorbital bones, are formed in connection with this canal.

Among these bones the membranous part of the antorbital bone will be formed far in advance of the other bones. In an approximately 10 mm long specimen a blastema begins to form below the anterior part of the infraorbital and antorbital lines. As earlier stated, the organs in these lines are primary neuromasts. In a 10.3 mm long specimen (fig. 45 A), a bone of an irregular

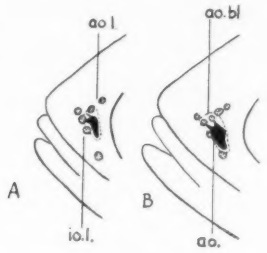

Fig. 45. *Leuciscus rutilus.* Antorbital bone. 40 ×. A: 10.3 mm. B: 10.6 mm.

appearance will form in this blastema, below three of the anterior neuromasts. At a somewhat later stage (fig. 45 B), both the blastema and the bone have grown in size, and both have spread out below some additional organs. The blastema and the bone lie immediately underneath the epithelium. The further development of the bone offers nothing of particular interest, up to the time when the fish has attained a length of about 18—20 mm. Then, the latero-sensory component begins to form, growing out as thin lamellae from the membranous part. As will be seen from a comparison between figs. 11 and 46, the latter component forms only in connection with the infraorbital organs.

As stated earlier, the infraorbital part of the canal will be formed far later than the antorbital portion, and since the formation of the latero-sensory component is dependent on the invagination of the canal, a fact pointed out by DEVILLERS, the infra-orbital bones will, consequently, form considerably later than the antorbital bone. Only in a 20 mm long specimen may a more or less continuous blastematic cord be perceived, but as yet no ossification has taken place in it. However, in a 22 mm long specimen the two hindmost bones have formed. At this stage, they have the same extent as in an adult, though being considerably narrower. In spite of the fact that, possibly, several organs participate in the formation of the blastema, the bone forms singly. No indication of any serial formation is traceable. The first infraorbital bone appears at the 24 mm stage, also as a whole. Later, in the course of the development, just before the canal is about to sink in, lamellae grow out from the bones which, as the canal sinks in and closes, continue to develop till, finally, they have surrounded the canal.

Bones formed in connection with the mandibulo-preopercular canal.

In connection with this canal, splenial bones, which usually fuse with the dental and angular bones, may appear in Teleosts, as well as a preoperculum and suprapreopercular bones.

In my analysis below of *Phoxinus* the various mandibular bones will be dealt with in detail. Since *Leuciscus,* in this particular respect, well conforms

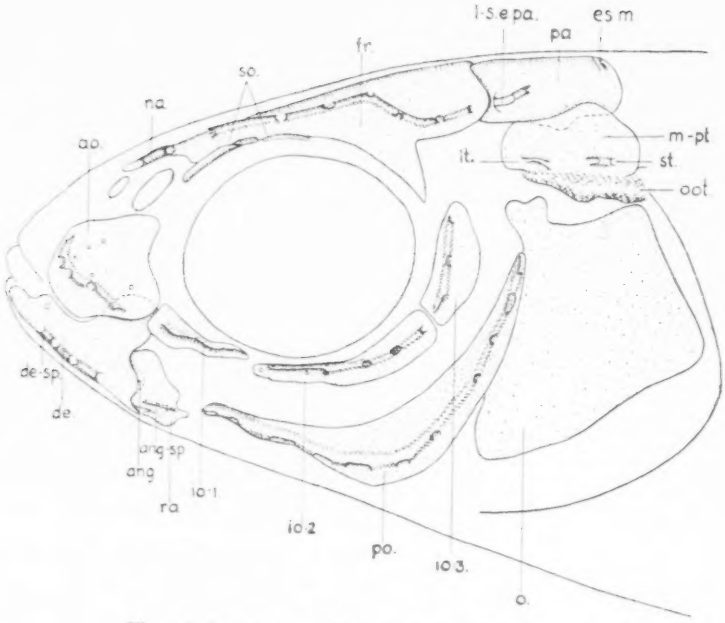

Fig. 46. *Leuciscus rutilus*, 44 mm. Canal bones. 13 ×.

to that fish, only a brief account of the mandibular bones in *Leuciscus* will be given here.

As in the other examined fishes, the dental bone is one of the first dermal bones that appear in the cranium. In a 6.5 mm long specimen, the bone begins to form and, as in the case of the other members of *Cyprinidæ*, it is, from the first, in its anterior part connected with MECKEL's cartilage. Then, the dental bone grows rapidly. Only the anterior portion will remain connected with the cartilage. When the fish has attained a length of about 20—22 mm, the splenial bones begin to form, in a way similar to that reported above with regard to the latero-sensory component in the frontal bone. From their first appearance, the bones are closely joined with the dental and angular bones, respectively. Thus, three splenial bones fuse with the dental, two with the angular bone. The bones form from the front backwards.

As the above described bones, also the preoperculum consists of two components, formed at different times. The first primordium of the lamellar component can be discerned in an 8.1 mm long specimen. (Fig. 9, *p.o.*), in the shape of a small chip of a bone, below two organs in the preopercular line. The bone has formed from a single blastematic cord which, at this stage, extends to the organ in front and backwards to the proximate caudal organ. In a somewhat bigger specimen, viz. 9.5 mm, the bone has grown markedly, chiefly forwards, while simultaneously becoming considerably broader. When the fish

has obtained a length of about 20 mm, the latero-sensory component begins to form, in connection with the invagination of the canal, assuming the shape of perpendicular lamellae growing out from the underlying membranous bones. Its appearance in the fully developed bone is shown in fig. 46. It is angular, with an anterior horizontal part, extending to the mandibular joint, and a vertical portion stretching half-way up on the cheek. The canal opens through eleven foramina in the bone into the epidermis. Suprapreopercular bones are missing in the examined specimen, but DEVILLERS (1947), states that the preopercular bones continue out on the operculum, in the same way as in *Alburnus*, as will be shown later. In all probability, the latero-sensory component in the operculum is a suprapreoperculum that has secondarily fused with the operculum.

Bones formed in connection with the temporal canal.

In connection with this canal two bones are formed, viz. the inter- and supratemporal ones which, at an early stage, fuse with one another and with the underlying cartilage-bones to an intertemporo-supratemporo-opisthoticum or pteroticum, i.e., according to early authors, the squamosal bone.

Like the other bones, also this one forms in two stages, and, as DEVILLERS remarks, the bones arise in the same way as the frontal one, i.e., first, a typical dermal bone arises, without any preceding blastematic formation in connection with neuromasts. Then a genuine latero-sensory component appears. Already from the beginning the membranous part has fused with the opisthoticum. It forms as a single bone. This occurs as the fish has attained a length of about 16 mm. Also here, the latero-sensory component appears much later, in connection partly with the two organs, i.e. the intertemporal organs, innervated by the otic nerve, partly with the organ innervated by the glossopharyngeal nerve, i.e. the supratemporal portion. From their first origination they are closely connected with the membranous component which, in its turn, is united with the perichondral opisthoticum. All the components fuse into one single intertemporo-supratemporo-opisthoticum.

From this summary account of the development of the canal bones in *Leuciscus* it emerges that, although they form in two separate stages, the two components are, as a rule, from the beginning closely allied to one another. Like DEVILLERS I have arrived at the conclusion that the lamellar part of the frontal bone and the pteroticum arise as normal dermal bones without any perceptible previous blastematic formation. Also the other canal bones form in two stages, the membranous portion far in advance of the other part. However, in the latter bones the membranous part originates in a blastema appearing immediately below the epidermis in connection with neuromasts. In combination with the same organ, also the latero-sensory component will later be

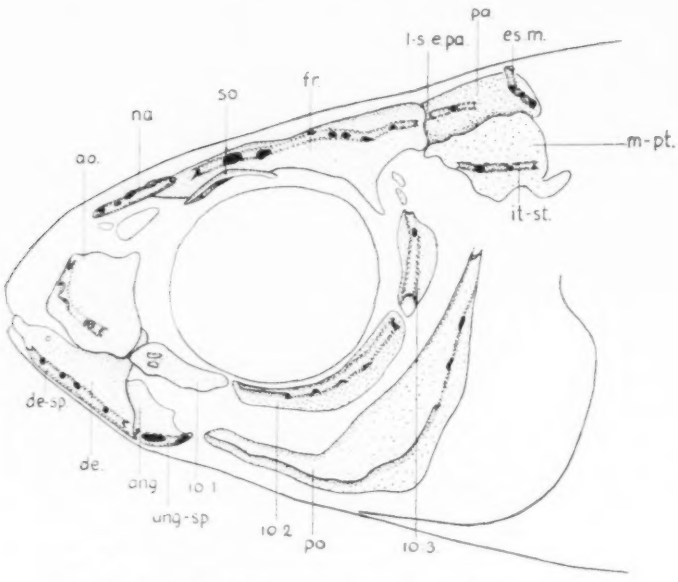

Fig. 47. *Abramis blicca*, 40 mm. Canal bones. 10 ×.

formed. In some of the fishes to be described below, this process of development is distinctly and easily observable and, for this reason, I shall return to this matter in later discussions.

2. THE CANAL BONES IN *ABRAMIS BLICCA* BLOCH.
(Figs. 27, 47.)

Since I have had only one stage (40 mm) at my disposal, I have not been in a position to study the development of the bones, but must limit myself to a brief account of the bones as they appear at this stage. The appearance and position of the bones will be seen from figs. 27 and 47. Their general aspect entirely conforms to that of the other Cyprinids. The lamellar and latero-sensory components have completely fused with one another into single bones. The latero-sensory component arises very much in the same way as in *Leuciscus*, i.e., from the first, in connection wich the lamellar part.

As far as the various bones are concerned, mention should be made of the fact that the nasal bone contains three neuromasts. In the frontal bone the latero-sensory part extends to the posterior edge of the bone. Also in the anterior part of the parietal bone such a component is to be found, closely fused with the bone. On the posterior portion of this bone, an extrascapular-medial bone (*es.m.*) has fused with it.

With regard to the infraorbital series of bones, an antorbital bone (*ao*) and

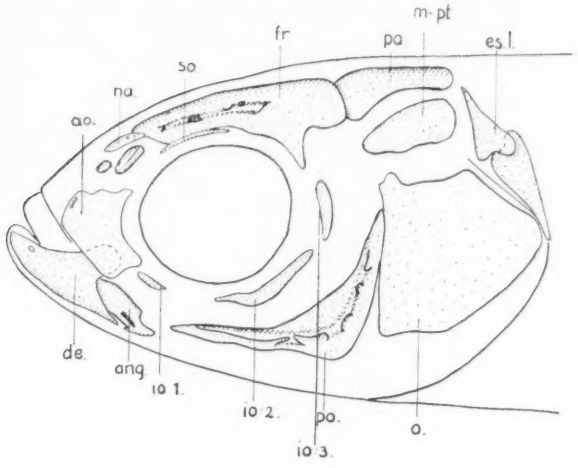

Fig. 48. *Alburnus alburnus*, 28 mm. Canal bones. 15 ×.

three infraorbital bones (*io*) are to be found, as in the previously described fishes. Behind the hindmost of these, there are two small bone lamellae, each immediately below an infraorbital neuromast of its own. They, later, fuse into a fourth infraorbital bone.

Six splenial bones have fused with the dental bone, two with the angular bone (*de-sp.*, *ang-sp.*). Along the whole of the preoperculum latero-sensory elements are noticed. The suprapreoperculum is missing.

In this species, as in *Leuciscus* and *Phoxinus*, the pteroticum consists of the opisthoticum, the membrano-pteroticum (*m-pt.*), two intertemporal bones (*it.*) and one supratemporal (*st.*), all these elements having fused into one single bone.

3. THE CANAL BONES IN *ALBURNUS ALBURNUS* L.
(Figs. 25, 48, 49.)

Since the bones form and develop in fundamentally the same way as in *Leuciscus*, only a brief account will suffice here. Also in this case, the bones develop in two stages, i.e. the membranous component will first appear, then, far later, the latero-sensory part forms. However, in *Alburnus*, the latter develops to some extent independently of the membranous part, though the two components will fuse at an extremely early stage of development. This is particularly conspicuous in the development of the frontal bone. Figs. 25 and 49 give a picture of the general appearance of the canal bones. Roughly, they conform to the corresponding bones in *Leuciscus*. Still, one detail should be referred to. On the operculum a latero-sensory component, containing a neuromast, is noticed. This canal portion constitutes a direct continuation of the

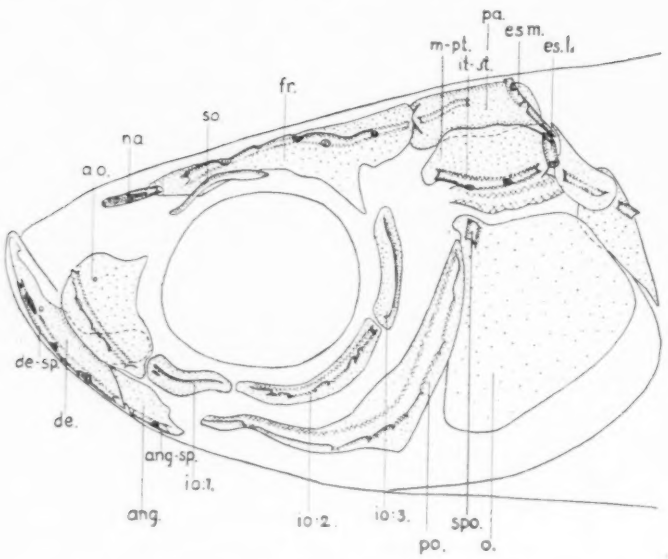

Fig. 49. *Alburnus alburnus*, 42 mm. Canal bones. 13 ×.

preopercular canal. In view of the known fact that the operculum does not contain any canal, the forementioned circumstance has to be regarded as a secondary phenomenon. In a 28 mm long specimen (fig. 48), the latero-sensory component in the preoperculum is well developed, while no such component is to be found on the operculum. As previously stated, the upper part of the preopercular canal develops extremely late in the Cyprinids, if at all. In this fish this part forms late. After the invagination a canal bone, which in this instance will fuse with the underlying operculum, appears round the neuromast. Thus, this canal bone is a suprapreoperculum that has fused with the operculum below it.

4. THE CANAL BONES IN *PHOXINUS PHOXINUS* L.

(Figs. 15—17, 21, 50—58.)

Bones formed in connection with the supraorbital canal.

The nasal bone.

The formation and development of the nasal bone in this fish are not easily explained in detail, since a varying number of neuromasts lodge in it. Thus, MANIGK (1933), reproduces three organs in the nasal bone, while I have found only two. Some young stages, however, suggest the possibility of a participation of more than two organs in the development of this bone. I have discovered

the first primordium of this bone in a 17.5 mm long specimen, below the organ 3 in the supraorbital line. There is as yet no indication that the canal is about to invaginate. The organs lie on the surface of the epidermis. At this stage, the nasal bone consists only of a small single blastema in direct connection with the posterior edge of the organ. In this blastema the first primordium of the bone is seen, and, like the blastema, it is single. The bone will remain at this stage of development until the fish has reached a length of 27 mm (fig. 17 a). It retains the same appearance and size. Below the two anterior pairs of nasal organs, no blastema can be observed. At the 35 mm stage (fig. 17 b) the bone has grown chiefly rostrad, but also, to some extent, caudad. The foremost of the nasal organs has, at this stage, given rise to the nasal pit-line, and, consequently, only two organs are left in the original primary nasal line. The bone has extended below the organ 3 and further to the organ 2. On the left side, two bone lamellae can be distinguished, one below each of the two organs. On the other side the two lamellae have fused into one bone, considerably narrower at the middle. This indicates a recent fusion. At the 47 mm stage (fig. 17 c) a first hint that the canal is about to invaginate is noticeable. The nasal bone has grown further rostrad, being now slightly gutter-shaped. In the adult (fig. 17 d), the nasal bone consists of a cylindrical bone round the anterior part of the supraorbital canal. In the examined specimen, two organs lie in each bone. In the left, there is a pore between the two organs. Such a pore is missing in the right bone.

From this it is evident that the variations in the development of the bone are considerable. Even in one and the same specimen the two bones may develop differently, and the number of organs lodged in them may vary from one specimen to another. As a rule, the two most caudal of the three nasal organs will, probably, form bones, while the foremost organ will, instead, give rise to the nasal pit-line. Further, two nasal bones are formed, one below each of the hindmost organs. However, these bones soon fuse into one bone.

At the 27 mm stage, a small blastematic aggregation, containing a small bone, is to be seen, a little caudally to the third right organ, immediately below the subcutaneous connective tissue. This blastema has no contact whatever with any neuromast. I have made the same observation at some younger stages, but not in any older ones. For this reason, it is impossible to obtain a more precise conception of this bone primordium. Possibly, it has fused with the nasal bone at some more advanced stage.

The frontal bone.

As seen from earlier references to the lateralis system, six neuromasts form the frontal part of the supraorbital line, though certain variations from this rule have been noted.

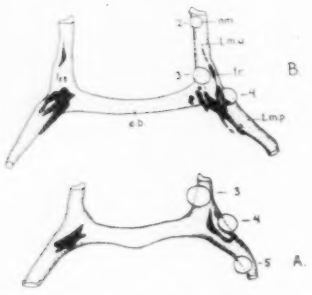

Fig. 50. *Phoxinus phoxinus*. Early development of frontal bone. 55 ×. A: 7.7 mm. B: 8.0 mm.

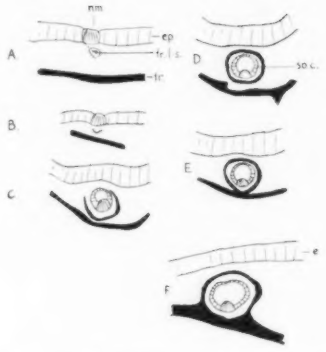

Fig. 51. *Phoxinus phoxinus*. Some development stages of the laterosensory part of frontal bone 50 ×. (Lamellar portion only partly drawn.)

The first primordium of the frontal bone has been noticeable at the 7.7 mm stage, in the shape of a small bone strip on the taenia marginalis, on a level with the epiphysial bridge, and in the proximity of the 4th frontal organ (fig. 50 a). At the immediately preceding stages (7.5—7.6 mm), no blastema is to be seen. The same applies to this stage. Beetween the taenia and the epidermis there are cells, sparsely distributed, and a diffuse net of threads of connective tissue. The first bone primordium forms in this connective tissue far from the organ. No breaking-down of the subcutaneous connective tissue below the organ has been noticed either at this or the preceding stages, nor any blastema in connection with the organs. At a somewhat later stage (8.0 mm, fig. 50 b), the frontal bone has grown considerably, but the ossification is not a regular process, ossicles forming irregularly everywhere in the connective tissue that extends along the taenia. A comparison between the right and left frontal bones at this stage discloses irregularities in the ossification. No marked similarity exists between these bones, apart from the fact that the ossification has proceeded approximately to the same extent rostrocaudad. In the description of the preceding stage it was pointed out that the organ 4 did not take part in the ossification. The same happens at this stage with the organ 3. The ossification takes place at a large distance from the organ. Nor in this instance are any blastemas formed. These various bone primordia fuse rapidly into one bone. This has occurred already at the 8.3 mm stage. At a slightly older stage, 9.4 mm (fig. 15), the frontal bone has assumed a fully normal appearance, extending below the whole row of frontal organs. As early as at this stage some secondary neuromasts have been added and, consequently, it is difficult to state to which particular kind this or that one belongs. At the next stage (47 mm) the two frontal bones have met. They partly overlap. In contrast with the

Cobitids and Silurids no fontanel is left open between them. The frontal canal has not, at this stage, as yet begun to form, but the other phase in the development of the frontal bone has set in. Below one of the neuromasts in the anterior third part of the frontal bone, the subcutaneous connective tissue has broken down. Immediately underneath the organ a small bone primordium has appeared, i.e. the first primordium of the latero-sensory component of the frontal bone. Below the other organs no blastema has as yet appeared. In another specimen, only 40 mm long, the formation of the latero-sensory component had advanced considerably more, and the entire process can therefore be studied in detail (fig. 51). The component round the first frontal neuromast was most developed, that round the last neuromast least. It is consequently possible here to follow the formation and development of this component in one and the same specimen, from the beginning up to full-grown state. The hindmost primordium, i.e. the least developed one, consists of a small, slightly gutter-shaped bone lamella below the organ (fig. 51 b). As yet, the organ has not begun to sink in. This small bone has no contact with the underlying membranous bone. It is entirely independent in relation to it. The next but hindmost latero-sensory component (fig. 51 c) surrounds two thirds of the canal, which has now sunk in. The component in front of it (fig. 51 d) entirely surrounds the canal, though still remaining free from the underlying bone. A short part of the foremost component, on the other hand, which also, cylindrically, encloses the canal, has begun to fuse with the underlying bone (fig. 51 e). In the course of their further development the two components fuse more and more. The condition in the adult can be seen from fig. 51 f. It is obvious from what has been said above that the latero-sensory component is formed quite independently and that it is only secondarily that it fuses with the underlying lamellar bone. The number of latero-sensory elements that, at this stage, form part of the frontal bone varies from one specimen to another. Most often 3—5 such elements are found.

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Bones formed in connection with the infraorbital canal.

As previously stated, the infraorbital canal is formed very late, i.e. only when the fish is practically full-grown. As a result, the bones pertaining to this canal become fully developed very late.

The antorbital bone.

The position of the anterior primary neuromasts in the infraorbital line will be seen from figs. 14, 15 and 16. In front of the eye, the line curves dorso-caudad between the eye and the nasal placode. As to the antorbital bone, it is formed in connection with the organs 1—4. These four organs can rather easily be identified up to, and including, the 9.4 mm stage. At the 11.5 mm

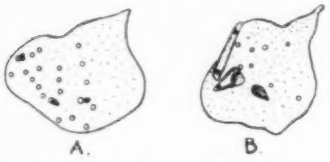

Fig. 52. *Phoxinus phoxinus*. Antorbital bone. 16 ×. A: 47 mm. B: 50 mm.

stage some secondary neuromasts have been added. Because of this, a definite identification becomes almost impossible.

The first primordium of the bone appears at the 7.9 mm stage, in the shape of a blastema immediately below the connective tissue. Unfortunately, the epidermis of this specimen (fig. 16 a) is somewhat injured and, for this reason, I have only been able to indicate the position of the organs 3, 4 and 5. From the reconstruction pictures of the three next stages (figs. 16 b, c, d), as well as from the histological one, it is clear that the organs 1, 2 and 4 are involved in the formation of the blastema. At these stages, the organs are somewhat irregularly distributed. At the 8.3 mm stage, a strip of blastema projects down towards organ 4, while the organs 1 and 2 lie directly outside the blastema. At the 9.4 mm stage a slightly different picture presents itself. There, the organs 2 and 4 lie on the blastema, while a narrow blastemic tongue protrudes up towards the organ 1. From these reproduced stages, as well as from some other specimens, it appears that the organs 1, 2 and 4 participate in the formation of the antorbital blastema, while the organ 3 does not seem to be implicated in this process. The blastema forms in immediate contact with the neuromasts. In spite of the fact that several neuromasts are engaged in the formation of the blastemas, the various blastemas will fuse and then give rise to a bone that is single from the beginning.

The earlier formation of this bone well conforms to that of the corresponding bones in *Amia* (Pehrson 1940). In that fish this bone is formed in connection with the organs 3—6 in the infraorbital line, i.e. four organs. Notwithstanding the participation of four organs in the blastematic formation, no serial ossification has been ascertained, the bone being single from the beginning. During the subsequent development the bone increases markedly in size, covering the anterior side of the cranium from the premaxillary-maxillary bones to the ectethmoid. The bone is practically as broad as it is long. A number of foramina for the latero-sensory nerves lead to the sense organs outside it.

The next phase in the development of the bone sets in when the fish has reached a length of 47 mm and the latero-sensory components begin to form. As yet, the canal has not commenced to sink in. It is therefore impossible to distinguish between primary and secondary neuromasts. However, below three of these organs small blastemas have formed immediately below the respective organs. The subcutaneous connective tissue below the organs is dissolved, and

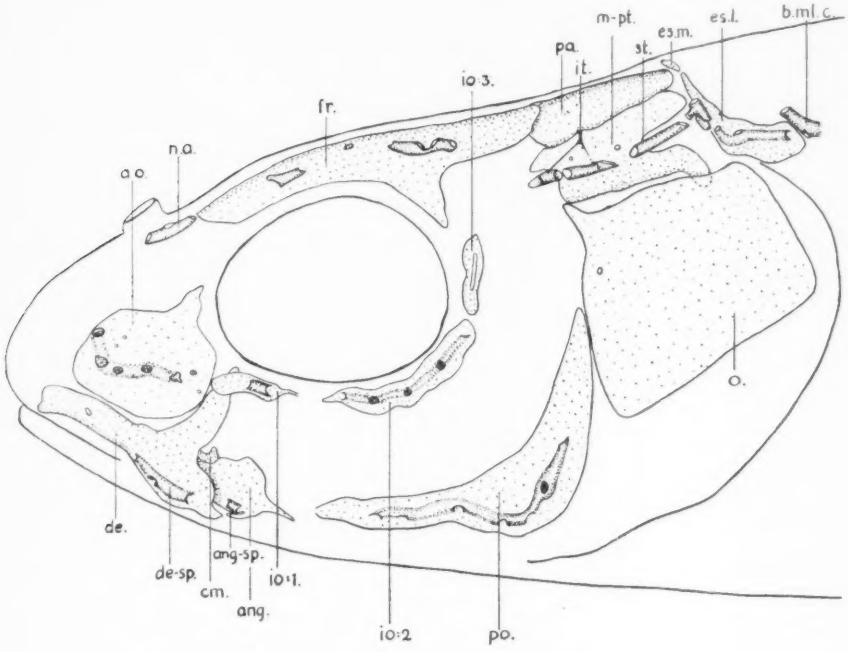

Fig. 53. *Phoxinus phoxinus*, 60 mm. Canal bones. 10 ×.

the histological picture reveals a pronounced cellular immigration, particularly from the parts immediately caudally to the neuromasts. For a detailed analysis, see below. The respective position of the three bone primordia will be seen from fig. 52 a. From that figure it is also obvious that the bones lie in immediate contact with the posterior end of the respective organ. The bones form quite independently, far from the lamellar part of the antorbital bone. Since, for reasons already mentioned, the particular neuromast cannot with certainty be identified, it is impossible to state definitely to which among the bone-forming neuromasts those of the younger stages correspond. All probability, however, suggests that these three neuromasts are analogous to the neuromasts 1, 2 and 4 in the younger specimens, i.e. the neuromasts that formed the blastema of the lamellar part of the bone. Here, the organ 3 probably forms part of the rostral pit-commissure.

At a somewhat later stage, 50 mm (fig. 52 b), the canal has sunk in and the small bone lamellae from the preceding stage have changed into three still mutually independent cylindrical bones. However, these bones have partly begun to fuse with the underlying lamellar bone. In an older specimen, 60 mm (fig. 53), the cylindrical bones have also fused into a unified bone tube, with openings for the canal pores. These openings indicate the boundary between

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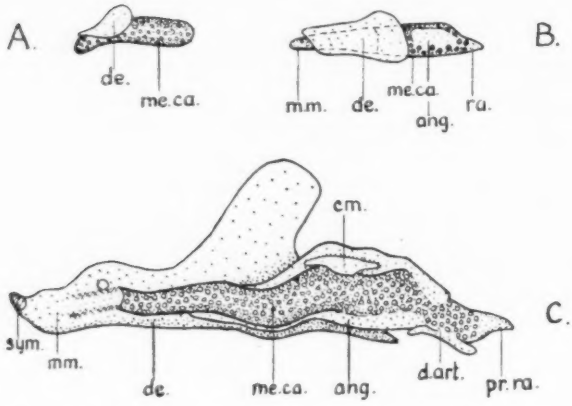

Fig. 54. *Phoxinus phoxinus*. Development of lower jaw. A: 6.0 mm, 60 ×. B: 7.3 mm, 60 ×. C: 17.5 mm, 50 × (from medial side).

the previously separate bones. In contrast with the two preceding stages, four latero-sensory elements appear in the reproduced specimen.

The infraorbital bones form extremely late, in comparison with the lamellar part of the antorbital bone. Only in a 35 mm long specimen has the middle of the three infraorbital bones begun to form, from a thin bone lamella in connection with two neuromasts. The anterior bone forms at the 47 mm stage, while the caudal appears somewhat earlier. Fundamentally, the bones form in the same way as the antorbital, with one exception, viz. that the difference in the time of the formation of the two components is considerably less and that the two components are from the beginning fused with one another.

Bones formed in connection with the mandibulo-preopercular canal.

Since the interpretation and terminology are vague, as far as the bones pertaining to the mandible are concerned, a matter referred to by HAINES, as late as in 1937, I propose in this connection not to limit myself to the canal bones only, but to deal also with the other bones in the mandible. Even today, the terminology lacks uniformity, different authors applying different terms to the same bone and the same term to completely different bones, a fact that complicates the interpretation of the literature on these subjects. Below, I shall, as far as possible, adopt the terms and interpretations suggested by HOLMGREN—STENSIÖ (1936).

In the youngest stage at my disposal (6.0 mm, fig. 54 a) Meckel's cartilage (*me.ca.*) consists of a slightly curved, almost cylindrical cartilaginous rod, of a uniform thickness. Processus coronoideus and retroarticularis are missing. The two cartilages meet rostrally in a faint symphysis. On the anterior point of the two cartilages, a mento-mandibular bone has already begun to form. Among

the dermal bones, only the dental is to be found, extending laterally along the anterior half of the mandible. Along its whole length it is more or less closely joined with Meckel's cartilage. Whether at some earlier stage, the dental bone has been independent and later, secondarily, fused with the underlying cartilage, I am not, at present, in a position to state definitely but, in all probability, this is not the case. In certain fishes, *Amiurus* (KINDRED 1919), *Esox, Salmo* (PEHRSON 1944 a), the dental bone forms independently, to fuse only later with the mento-mandibular bone. In *Cyclopterus* (UHLMANN 1921), the bone is formed in contact with the perichondrium. At the 7.3 mm stage (fig. 54 b), the mandible, roughly, retains the same general appearance. However, a processus retroarticularis has formed. This has already begun to ossify at the point of attachment of a strong ligament that extends to the suboperculum. The dental bone has grown caudad, covering, now, about two thirds of the mandible. The posterior third is free from the underlying cartilage. Between the posterior edge of the dental bone and the processus retroarticularis a new ossification has formed, in contact with the cartilage angulare (*ang.*). The anterior and upper edge of the ossification is free. In other fishes, e.g., *Esox* (PEHRSON 1944 a), this bone forms independently fusing only during a late phase of development, in a small area, with the underlying cartilage.

At the 17.5 mm stage (fig. 54 c), fairly considerable changes have begun, and two new bones have been added. In the anterior part Meckel's cartilage has continued to ossify. The anterior point consists of bone, and the cartilage is completely resorbed (mm). In the caudal part the angular bone has begun to invade the cartilage. Also, the entire processus retroarticularis has ossified. Apart from these two ossifications, an additional one has appeared in this part of the mandible. This new ossification, the dermarticular bone (*d.art.*) is situated on the ventral side, distinctly separate from the other two. For a short distance, the bone is fused with the cartilage. Rostrally and caudally lamellae project. In *Salmo*, ventrally to the articular bone, a separate bone forms, which later will fuse with it. HOLMRGEN—STENSIÖ regard this bone as a dermarticular one. Several authors make no distinction between the dermarticular and the angular bone. Thus, the two terms have become synonymous. But, as shown by HOLMRGEN—STENSIÖ, this is erroneous. The two terms refer to entirely different bones.

The second new ossification is at this stage visible on the dorsal side of the mandible, medially to the middle of the angular bone (*cm.*). Already at the 9.4 mm stage, a considerable thickening has become perceptible in this place, and an ossification has formed. At somewhat older stages, this ossification extends both on the medial and lateral side of the mandible. Only later, lamellae commence to form, first the part directed caudad (11.5 mm), then the rostral part (16 mm).

In the Cyprinids, this bone is without exception well developed. I have found

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it in all examined Cyprinids. In the Characinids examined by me, viz. the *Sarcodaces* and *Alestes*, the bone is very feebly developed, no lamellae have developed. In *Nemachilus* (see below), there is one bone in a corresponding position, but it forms independently and does not fuse with the mandible. This bone has been interpreted differently by different authors and is met with in the literature under various names. It was first mentioned in *Perca* (CUVIER and VALENCIENNE 1828) and called "operculaire", as it was considered to be homologous with a bone of the same name in the reptiles. In 1846, OWEN describes this bone in *Arapaima* and, instead of the forementioned term for this bone, which might easily cause it to be mistaken for another bone in the fish cranium, he suggested the name splenial. In his work on *Gymnarchus*, ERDL (1847), called the same bone *der Kronenfortsatz des Unterkiefers* or pars coronoidea mandibulae. In 1878 VETTER described it in *Esox* as a *Sesamoidverknöcherung an der Insertation der Endsehne von A_3—$A_2{}^t$ an Meckelschen Knorpel.* (A_3 is the third portion of m. adductor mandibulae, $A_2{}^t$ its ligament). In the same year COPE described it in *Belone* as the coronoid. In his opinion, this bone was not to be found in any Teleost family, with the exception of the Belonidae. Finally, RIDEWOOD (1904), proposed the term "sesamoid articular". In 1916, STARKS described this bone in a great many different fishes, applying to it the term suggested by RIDEWOOD. None of the forementioned authors have studied the ontogenesis of the bone but limited their observations to adult material. For his own part, STARKS expresses doubts as to whether there exists any question here of a sesamoid ossification, but, to judge from his later comments, he seems to regard it as such. He examined a number of fishes of different families, and in the majority he was able to ascertain the presence of this bone. Summarizing, he states inter alia: "The sesamoid articulare is variable in position, though it is always in relationship with Meckel's cartilage, usually in very close association with it." He adds: "The sesamoid articular is, doubtless, as its name implies, a sesamoid bone." From STARKS' descriptions it will be noted that, in different fishes, the bone may either be a separate dermal bone or more or less closely fuse with the underlying cartilage. From the above account of the formation and development of this bone in *Phoxinus*, it is evident that, at least in this fish, there is no question of a sesamoid but of a dermal bone, formed in direct contact with the cartilage. In this instance, the name "sesamoid articular" is unsuitable. I prefer the term corono-meckelian which, according to DE BEER (1937), after BÖKER (1913), "arises where the fibres of the adductor mandibulae muscle are inserted on the processus prearticularis of Meckel's cartilage, as an ossification of these fibres and of a perichondral lamella which spreads over the cartilage". The description refers to *Salmo*.

The next phase in the development of the mandible begins with the 27 mm stage, when the splenial bones are about to form. At this stage, the subcutaneous

connective tissue begins to dissolve below the mandibular sense organs and the blastemas to form. Along the future canal the epithelium has begun to thicken and to sink in, in the shape of a keel. At the 35 mm stage, the canal has closed on one side, with a narrow lumen, while, on the other side, no canal has appeared. It is the foremost organ in the mandibular line that has invaginated. Round this canal portion lies a splenial bone, consisting of two lamellae, one medial and one lateral (fig. 18). These lamellae lie free in the subcutaneous connective tissue, without any contact with the underlying dental bone. At the 47 mm stage, the two lamellae have fused into a cylindrical bone round the canal (fig. 19). The splenial bone remains completely free. At this stage, also the first primordium of the angular-splenial bone has formed, in the shape of a small strip of bone behind the caudal point of the dental bone, laterally to the angular. In a slightly older specimen an additional bony strip appears and, consequently, also the primordium of this splenial bone is binary. At the 50 mm stage, the splenial bone has fused with the dental into a dental-splenial bone. The morphological picture entirely agrees with that of the majority of the examined Teleosts. The number of dental-splenial bones in *Phoxinus* varies from one specimen to another. One of the two oldest specimens has only one splenial bone, while the other has two. In a specimen, described and reproduced in 1933 by MANIGK, there are three neuromasts in this part of the canal and therefore, in all probability, three splenial bones. The angular-splenial bone is subject to the same development. First, a cylindrical bone is formed round the canal, and only then does this bone fuse with the underlying angular bone.

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The similarity in the formation of these bones in *Phoxinus,* on one hand, and *Amia* (PEHRSON 1940) and *Polypterus* (PEHRSON 1947), on the other, is obvious. In a 24 mm long specimen of the latter fish, the splenial bones are separate cylindrical bones round the mandibular canal but later fuse with the underlying dental bone. In the former fish the splenial bones are not separate, but the blastemas form independently and, at an early stage, the splenial bones are only partly fused with the dental bone. Also in this species, the splenial bones form with a medial and a lateral lamella.

The dental bone in the Teleosts has been regarded by several authors (HOLMGREN—STENSIÖ 1936, PEHRSON 1944 a, and others) as a dental-splenial-mento-mandibular bone, i.e. a complex bone with three genetically different components. However, in the Teleosts, so far examined, no separate splenial elements have proved ascertainable. From the first, they have fused with the dental bone. For this reason, some authors have doubted whether the dental bone would actually be composed of dental and splenial elements. Thus, DE BEER (1937), writes, regarding the dentary in *Salmo,* as follows: "In the absence of evidence of separate ossification of the bone surrounding the canal, the whole bone cannot be called a dentalo-splenial, but must be regarded as a

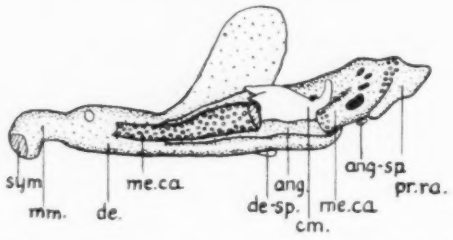

Fig. 55. *Phoxinus phoxinus*, 47 mm. Lower jaw from medial side. Part of Meckel's cartilage is omitted. 25 ×.

dentary which has acquired relations with the lateral line canal, or a splenial which has taken the dentary's place." On the other hand, PEHRSON (1944 a), says about *Esox:* "No separate splenial elements are formed in the pike, but in the 18.8 mm specimen a strip of comparatively sparse blastematic tissue is seen along the ventro-medial side of the dental. This blastema is the homologue of the splenial primordia which are comparatively independent in *Amia* (PEHRSON 1940). — — — From the description now given of the development of the so-called dental (dentary) in *Esox* it is evident that this bone in *Esox*, and probably in Teleosts generally, is a complex *os dentale-mento-mandibulare-spleniale*." The account of the formation and development in *Phoxinus* of the dental and splenial bones makes it obvious that these two elements form and develop entirely independently of one another, the former as a bone of double origin (dermal-cartilage), the latter as a latero-censory canal bone. Only at a comparatively late stage of development will these two components fuse, and the final result will be the same as in, e.g., *Salmo* and *Esox*, irrespectively of certain ontogenetic differences. From this it is clear that PEHRSON's above-cited conception must be correct, considering, further, that there is no reason to suppose that, in this respect, *Polypterus, Amia, Phoxinus, Tinca* and *Nemachilus* would differ from all other examined bony fishes.

As far as the other bones in the mandible are concerned, no noteworthy changes have taken place. Their general appearance can be seen in fig 55.

However, one problem should be discussed in this connection, viz. the relationship between the articular and the angular bone in the Teleosts. After an examination of some adult fishes the above-quoted HAINES (1937), arrived at the conclusion that "in most Teleosts (*Mugil, Sardinia, Trigla*) the articular is absent and the angular invades the perichondrium and cartilage to form the joint surface". The weakness of HAINES' examination and conclusion lies in the fact that only adult material was analysed and the genesis of the bones disregarded. The development of the posterior part of Meckel's cartilage in *Phoxinus* apparently confirms HAINES' views. As stated in the previous descriptions of stages, an ossification, which later will partly grow forwards below the dental bone, and partly invade the cartilage in the mandible, appears

already early on the lateral side of the posterior part of the mandible. Apart from this ossification, there are in this region only two, viz. the dermarticular and the retroarticular bones. These facts can, of course, be interpreted in different ways. Either the angular bone has invaded the cartilage, forming the mandibulo-quadrate joint or this ossification is an articular bone growing forwards with a lamella, thus replacing the angular bone, or these two bones form both together part of the ossification. It is difficult to state definitely which of these three possibilities applies to *Phoxinus*, but to judge from some examined fishes a typological series can be arranged, according to which the angular bone in more differentiated fishes would replace the articular. In *Amia* and *Lepidosteus* there is a well developed articular bone which, however, is comparatively small, as compared to that of their ancestors among the paleozoic fishes. In the more primitive Teleosts, such as *Elops, Megalops, Albula*, etc., (HAINES 1937), the articular bone still remains as a small separate bone. In addition, there is an angular ossification. In more advanced fishes, only one ossification, apart from the retroarticular bone, is to be found in this region, viz. the angular ossification. From this it is obvious that it is the articular bone that disappears and the angular that invades the cartilage, being in this manner substituted for the former. From the above description of the condition in *Phoxinus* it is evident that there is only one ossification on the lateral side, viz. the angular. There is, in this region, no separate ossification that can be interpreted as an articular bone. Furthermore, the splenial bone that forms in this area fuses with the underlying bone. Since, to our knowledge, splenial elements do not fuse with the articular but with the angular bone, this offers an additional indication that this bone is an angular. In my opinion, the embryological data regarding this fish confirm HAINES' theory that the articular bone is absent in more specialized Teleosts.

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The preoperculum.

In a young specimen (7.3 mm, fig. 14), the preopercular pit-line consists of eight primary neuromasts. The fact that the mutual position of the neuromasts varies from one specimen to another, and that, further, the number gradually increases, complicates any attempt to identify these neuromasts. At the 7.1 mm stage (fig. 56 a) a blastema extends below four neuromasts. The blastema is well delimited, and situated immediately below the epithelium, in a direct contact with the organs in question. In this blastema, in which no indication of a serial formation is noticed, the first primordium of the preoperculum has appeared, in the shape of a thin bone lamella below two of the organs. The bone does not show any sign of ossification from different centres. At slightly older stages (7.3, 7.5, 9.4 mm, figs. 56 b, c and d), the blastema can be observed to grow rostrad and to some extent, also caudad, below an increased number

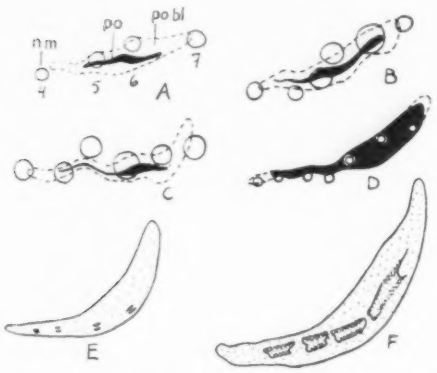

Fig. 56. *Phoxinus phoxinus*. Some development stages of preopercular bone. A: 7.1 mm, 80 ×. B: 7.3 mm, 80 ×. C: 7.5 mm, 80 ×. D: 9.4 mm, 50 ×. E: 47 mm, 8 ×. F: 55 mm, 8 ×.

of organs. At the same time, also the bone grows, correspondently. At the 9.4 mm stage, the main part of the blastema has ossified. Only at the two ends of the bone, there is still some blastema left, constituting a zone of growth for the bone. As in the case of the other canal bones, the second phase of the formation of the preoperculum sets in considerably later. In a 47 mm long specimen (fig. 56 e), the latero-sensory component has begun to form, in connection with four of the preopercular organs. Simultaneously with this process, the usual breaking-down of the subcutaneous connective tissue can be traced, as well as the formation of a blastema in immediate contact with the neuromasts. As in the mandibular part of the line, also these bones are, as shown in the figure, from the beginning, binary. These binary primordia fuse with one another, forming, as the canal begins to invaginate, a cylindrical bone round it. The latest component fuses comparatively soon with the underlying lamellar part of the preoperculum (fig. 56 f). Only in older specimens have the latero-sensory components fused with one another into one tube (see fig. 53). The number of canal bones that make up the preoperculum varies. Generally, they seem to amount to four. Occasionally, there may be six. In this fish, the preopercular canal is very short. For this reason, the canal bones do not extend along the entire bone, but, chiefly, only in the anterior horizontal part of the bone.

Bones formed in connection with the temporal canal.

As previously stated, a complex bone, consisting of three genetically different components, viz. a cartilage-bone, a membranous bone and three canal bones, will develop in connection with this canal. In the course of the development, all these bones will fuse into one complex bone. In *Phoxinus*, the conditions

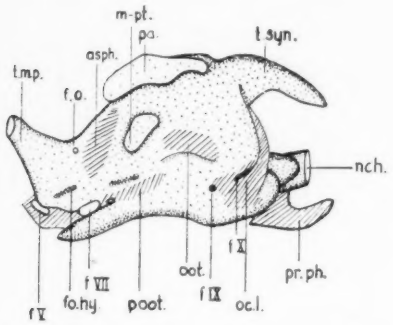

Fig. 57. *Phoxinus phoxinus*, 16 mm. Posterior part of skull. 23 ×.

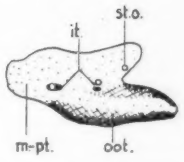

Fig. 58. *Phoxinus phoxinus*, 47 mm. Pterotic bone. 16 ×.

easily allow an analysis of this process, since all the components, from the beginning, form separately in relation to one another.

In a 16 mm long specimen (fig. 57), there are two dermal bones in the otic region, one parietal bone (*pa.*) on the dorso-lateral side, and, ventrally to it, on the lateral side, a minor dermal bone, the membrano-pteroticum (*m.-pt.*). This bone is entirely separate in relation to the underlying cartilage. The bone forms, without any previous blastematic formation in the subcutaneous connective tissue, like a typical dermal bone, in the same way as the parietal bone. Fig. 57 will, further, show such parts of the cartilage in the otic region as have ossified (indicated by oblique stripes). Thus, it is possible to distinguish the autosphenoticum (*asph.*), the prooticum (*poot.*), the opisthoticum (*oot.*) and, further back in the cranium, the ex-occipital ossification (*oc.l.*). In this connection, the opisthoticum is of particular interest among these cartilage-bones. In a slightly older specimen, this ossification has extended further rostrad, while, at the same time, the membrano-pteroticum has grown caudad. In the course of this process, the two bones fuse with one another.

The latero-sensory component begins to form at the 47 mm stage (fig. 58), in connection with the two intertemporal organs. Immediately below these organs, first, a blastema and, then, a bone forms independently of the underlying bone. Below the supratemporal organ, no blastema has, as yet, formed. In a 60 mm long specimen (fig. 53), the canal has been invaginated, and the latero-sensory bones have developed into three cylindrical bones. The caudal intertemporal and the supratemporal bones have fused with the underlying bone, while the anterior intertemporal bone still remains independent. In another examined specimen, the two intertemporal components have fused with one another, as well as with the underlying bone, while the supratemporal bone remains free. The final result of this process is, accordingly, a complex bone consisting of a cartilage-bone, the opisthoticum, a membranous bone, the

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membrano-pteroticum, and, in addition, two intertemporal and one supratemporal latero-sensory element.

5. THE CANAL BONES IN *TINCA TINCA* L.

(Fig. 29.)

I have had at my disposal only one stage, 46 mm, but owing to the fact that, at this stage, the canal bones are being formed, it is possible to obtain a good impression of the way in which these bones form and develop. As to their formation these bones agree with those in *Phoxinus*, in so far as the latero-sensory component forms separately and, then, secondarily, fuses with the underlying bones.

The nasal bone (*na.*) consists, at this stage, of three small bone lamellae, each immediately below a neuromast. In the adult, these three bones fuse into one unified tube-shaped bone.

The lamellar part of the frontal bone (*fr.*) is well developed. At this stage, the latero-sensory parts of the same bone (*fr.l.-s.*) show different degrees of development. This component consists of ten separate bones. The six foremost are most advanced in development, enveloping the, in this place, invaginated canal. The hindmost of these bones have begun to fuse, for a short distance, with the underlying bones. Further back, there is an additional row of but slightly developed canal bones, amounting, at this stage, to five, the hindmost lying on the parietal bone. Also these bones form as single ones, and in a direct connection with their respective neuromasts. In the adult, these bones have fused with the frontal and parietal bones, respectively. From the conditions in *Tinca*, it is evident that the latero-sensory component in the parietal bone forms entirely separately and only secondarily fuses with it, in the same way as the medial extrascapular bone.

In the infraorbital row of bones, the lamellar part of the antorbital bone is well developed, as are the two foremost infraorbital bones. The third infraorbital bone is very feebly developed. In the antorbital bone, the latero-sensory component has begun to form in connection with the two canal portions that are to be found within this area. These canal bones are independent of the lamellar bone. Between these two comparatively well developed canal bones, an additional recently formed bone, immediately below a neuromast, is to be noted. The development of this bone proves that the canal bones in this region have no binary origin. In a full-grown fish, the canal bones have fused with the underlying bone.

As stated in the description of the lateral line system, there was a yet no mandibular canal in that specimen. Some authors have in fact denied the very existence of any such canal in this fish. None the less, there is in this specimen a single splenial element, in connection with a mandibular neuromasts, situated

far from the dental bone. In a full-grown *Tinca*, separate splenial bones are to be found round the mandibular canal.

The canal component of the preoperculum has advanced rather far in its development. Some of the cylindrical bones are still binary, which shows that these canal bones originate from binary primordia. The two foremost bones are independent, while those behind them have fused with the lamellar part.

In connection with the organs in the temporal part of the canal, three single canal bones have just appeared (*it.st.*), constituting the latero-sensory component in the pteroticum. In addition, this bone is composed of a fused opisthoticum and membrano-pteroticum. In the adult, all these components have joined into one single bone.

In sum, with regard to the formation and development of the canal bones, this fish may be said to occupy a position between *Phoxinus* and *Nemachilus*, since the latero-sensory component forms independently in relation to the underlying bone. This component may either fuse with the lamellar part (*Phoxinus*-type) or remain separate in relation to that part (*Nemachilus*-type).

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6. THE CANAL BONES IN *NEMACHILUS BARBATULA* L.

(Figs. 59—66.)

In the introductory remarks, mention was made of the fact that the canal bones in the Cobitids have not before been investigated or not even reproduced or referred to, in works dealing with the cranium of these fishes (SAGEMEHL 1891, CHRANILOV 1927). The explanation is, perhaps, that these bones, at least in this particular species, lie free in the skin and that, for this reason, they have been overlooked. Unlike the conditions in the previously described fishes, the latero-sensory bone components remain free also in adult specimens.

Bones developed in connection with the supraorbital canal.

The nasal bone develops in connection with the anterior separate part of the supraorbital canal. In a 33 mm long specimen the first primordium of the nasal bones can be found below the two nasal organs. At this stage, the canal has not yet sunk in. Underneath the foremost organ (fig. 59, *na.*), a thin bone lamella has formed, divided in two tongues below and behind the organ. In this slit the nerve runs to the organ. Below the other organ only a blastema has formed (*na.pr.*). The same applies to *Salmo salar* (PEHRSON 1944 a), in which "the bony nasal primordium is formed in one piece, but with a very deep longitudinal indentation". In a specimen, 47 mm long, the canal is invaginated and the two nasal bones have changed into two tube-like bones round the canal. These bones do not fuse, and even in the adult (fig. 60, *na.*) the two bones remain independent.

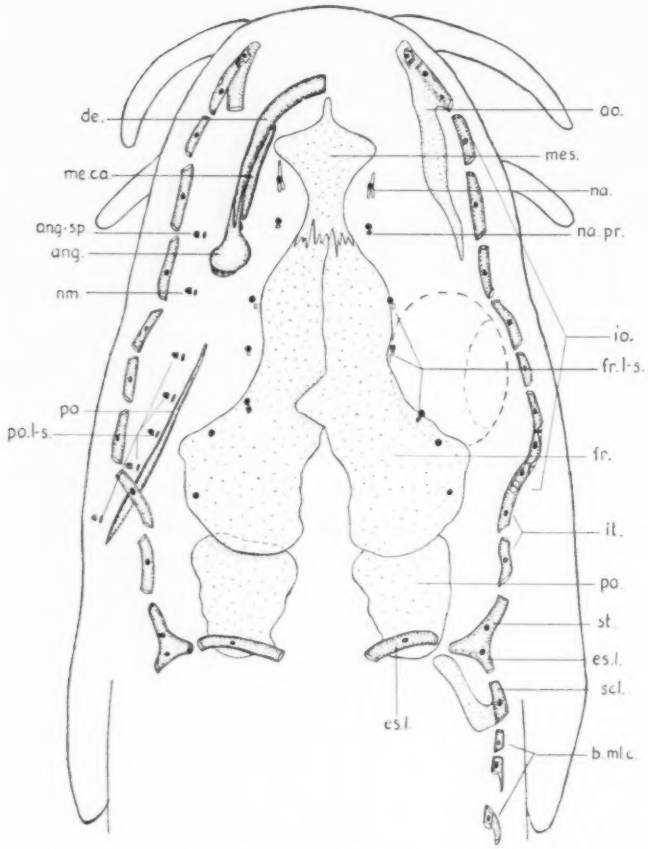

Fig. 59. *Nemachilus barbatula*, 33 mm. Skull from dorsal side with canal bones. 16 ×.

The frontal bone. The first primordium of this bone appears in a 5.5 mm long specimen, in the shape of a comparatively well delimited blastema below the organs 5 and 6 in the supraorbital line (fig. 61 A). The blastema is broadest above the epiphysial bridge, narrowing forwards and backwards. In a 6.0 mm long specimen (fig. 61 B), the blastema has developed rostrad, extending almost up to the organ 3. The blastema continues to be broadest above the epiphysial bridge. Bone lamellae have formed in connection with the organs 4, 5 and 6. On the left side they still remain separate, but on the right side, below the organs 5 and 6, the lamellae have fused. The bone below the organ 4 is still independent. In a 6.6 mm long specimen (fig. 61 C), the blastema retains approximately the same extent, but the blastemic strips above the epiphysial bridge have grown markedly, approaching one another. On the left side the lamellae below the organs 5 and 6 have fused, and the lamella beneath the

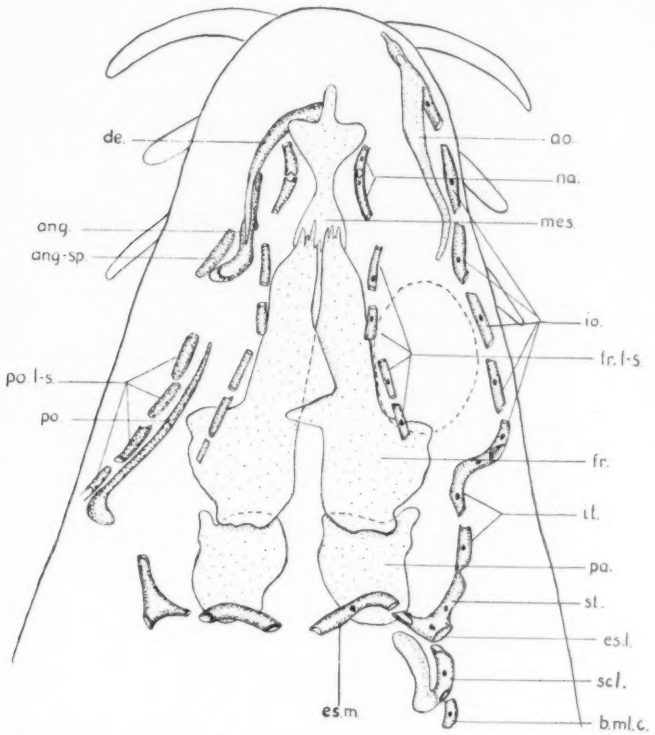

Fig. 60. *Nemachilus barbatula,* 70 mm. Skull from dorsal side with canal bones. 8 ×.

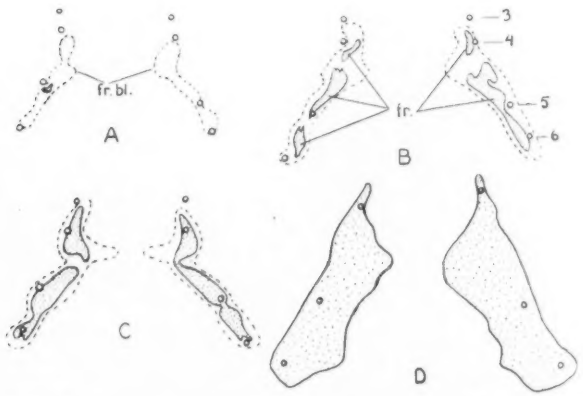

Fig. 61. *Nemachilus barbatula.* Development of lamellar part of frontal bone. A: 5.5 mm, 50 ×. B: 6.0 mm, 60 ×. C: 6.6 mm, 55 ×. D: 9.3 mm, 55 ×.

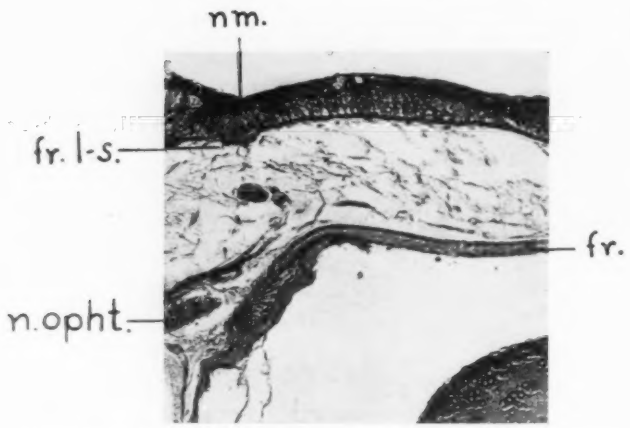

Fig. 62. *Nemachilus barbatula*, 33 mm. Third neuromast in supraorbital canal with first primordium of latero-sensory component of frontal bone. Microphoto 150 ×.

organ 4 has increased pronouncedly in size. On the right side all the three bones have fused. Nevertheless, because of the fact that the bone in two places is considerably narrower, the three original bones are still clearly distinguishable. In a 9.3 mm long specimen (fig. 61 D), the bone consists of a single disc of a comparatively uniform breadth. The different components can no longer be discerned. In a 12 mm long specimen, the two frontal bones have met, on a level with the epiphysial bridge.

In spite of the fact that the subcutaneous connective tissue is well developed at these young stages, I have been unable to notice any breaking-down below the organs or any signs of cellular immigration, a feature which is a marked characteristic later, at the formation of the latero-sensory component.

The next step in the development of the frontal bone begins in a 33 mm long specimen, when blastemas and bones form below the organs 3, 4 and 5 (fig. 59, *fr.l-s.*). The neuromasts still lie superficially, and the canal has not, so far, begun to invaginate. In contrast with the conditions prevailing at younger stages, a distinct breaking-down of the basal membrane, as well as a well delimited blastematic formation in immediate connection with the neuromasts, are noticeable (fig. 62). Below the organs 3 and 4, a small bone has formed (fig. 59). Below the organ 5 only a blastema is to be found and, finally, below the organ 6 no sign of any blastema. When the fish has reached a length of 47 mm, the canal has invaginated. Round the canal, four cylindrical bones have formed, each connected with one neuromast. Sometimes, also a fifth bone may form (fig. 60). These canal bones do not fuse with one another, nor with the underlying membranous portion of the frontal bone. Thus, a fully developed frontal bone in this fish (figs. 60, 63) consists of two entirely independent

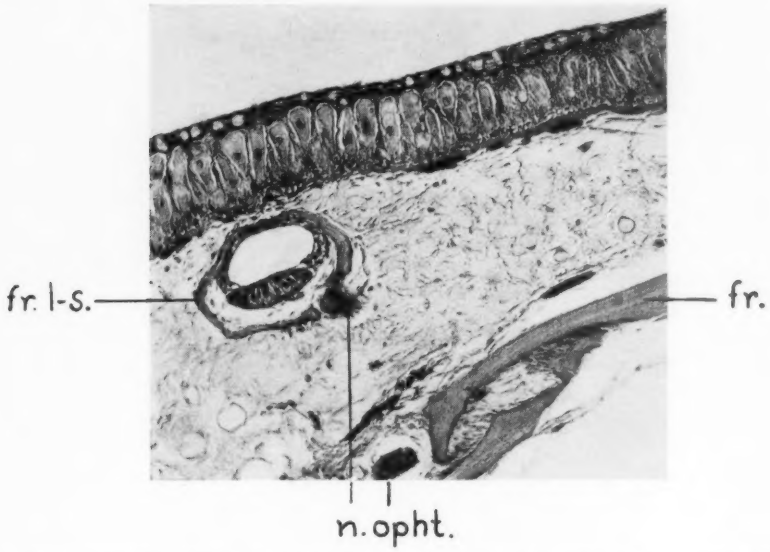

Fig. 63. *Nemachilus barbatula*, 47 mm. Third neuromast in supraorbital canal with fully developed latero-sensory component. Microphoto 150 ×.

components, viz. a lamellar part, and a latero-sensory one that in its turn is composed of 4—5 independent tubal bones.

Bones developed in connection with the infraorbital canal.

As previously stated, concerning the development of the lateralis system, in contrast with the conditions in the other examined fishes, the infraorbital canal in *Nemachilus* forms earlier than the other canals. As a result of this, the bones that form in connection with this canal will also appear earlier than the other canal bones.

The antorbital bone. In a 9.3 mm long specimen (fig. 64 A), this bone has formed and already developed comparatively far. In my nearest preceding younger specimen, 9.0 mm, there is no indication either of any blastema or any bone. In the 9.3 mm specimen the blastema lies immediately below the epidermis in connection with the two foremost organs in the infraorbital line, extending up towards the anterior external nasal opening. In the blastema a thin bone lamella has formed. The anterior portion of this lamella is well developed, while, in its posterior part, it is diffuse, and composed of fine bone strips. In a 12 mm long specimen, the bone has grown markedly caudad, reaching with its posterior part to the rostral portion of the ectethmoid bone. The general appearance of the bone will be seen from fig. 64 B. In the anterior portion of the bone, there is a foramen for a nerve to the organ in the infraorbital

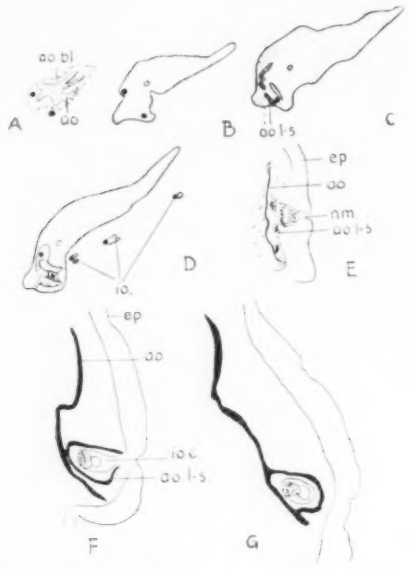

Fig. 64. *Nemachilus barbatula*. Development of antorbital bone. A: 9.3 mm, 70 ×. B: 12 mm, 28 ×. C: 14 mm, 33 ×. D: 21 mm, 20 ×. E: 14 mm, 60 × (dotted line in C denotes position of E). F: 21 mm, 60 ×.

canal. In a 14 mm long specimen (fig. 64 C), the bone has grown further in size. In addition, binary bony primordia, constituting the first rudiment of the latero-sensory component, have formed below the two foremost neuromasts. Below the sense organ 1 the dorsal bone primordium is directed dorso-caudad, the ventral one ventro-caudad. Below the organ 2, the two bone primordia are parallel. As will be noticed from the transverse section of fig. 64 E (the section marked by a dotted line in fig. 64 C), the binary latero-sensory component lies immediately below the neuromast, each bony primordium being surrounded by a well delimited blastema. Further, it appears that the bony primordia are free in relation to the underlying bone. In a 21 mm long specimen, the bone retains, roughly, the same appearance. However, the latero-sensory components have fused and the bones now surround the greater part of the almost fully developed canal. As will be seen from fig. 64 F, the canal component is still entirely independent. In a 26 mm long specimen, the bone has obtained its definite shape. Here, the two components have completely fused both with one another and with the underlying bone (fig. 64 G). The canal, which is now fully developed, is entirely surrounded by the tube-like bones, with the exception of three openings for pores to the surface of the epidermis. One pore opens out dorsally to the anterior edge of the bone, another rostrally, and the third caudally. In the adult fish (fig. 60), the bone has, fundamentally,

the same appearance as in the 26 mm stage, except that it has grown in length, this increase being particularly accentuated caudad.

The infraorbital bones. In the previously examined fishes, the infraorbital bones consist of a lamellar portion and a canal part that grows out from the former. The number of bones is small, generally not exceeding three. In this fish no lamellar portion appears. The bones consist exclusively of the canal part. Further, the bones are more numerous, but their number is inconstant, varying from one specimen to another. Even in the same specimen the number on the right side may differ from that on the left. The number varies from 4 to 7. The bones form from the front backwards.

In a 21 mm long specimen, only the three foremost bones have formed (fig. 64 D). Below the organ 3 in the infraorbital line a binary bone primordium has appeared. Below the organ 4, there is a single bone primordium, divided in its posterior part, which may indicate an earlier binary origin. Finally, below the organ 5, a single bone primordium is to be seen. All the subsequent bones will, likewise, form as single ones. In a 23 mm long specimen, no further infraorbital bones have formed, while single blastemas have formed below the other infraorbital organs. In a 26 mm long specimen, all the bones have formed. The subsequent bones are more or less tube-shaped. At the 33 mm stage, the bones are fully developed, and completely surround the canal. There is no hint of any lamellar component in them (fig. 59).

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Bones formed in connection with the mandibulo-preopercular canal.

The development of the mandibular bones will appear from fig. 65 A—G. Roughly, the development in this fish agrees with that in *Phoxinus*. Already in a 4 mm long specimen (Fig. 65 A), the dental bone appears in the shape of a small bony lamella in the anterior part of Meckel's cartilage. Right from the beginning this bone is fused with the cartilage. The next bone in the mandible forms when the fish has reached a length of 5.5 mm (fig. 65 C). It is a small thin bone lamella, originating in a blastema between Meckel's cartilage and the dental bone. The bone lamella is independent in relation to the two latter bones. This is the first primordium of the angular bone. At the subsequent stage, 6.0 mm (fig. 65 D), the bone has grown considerably, but it still remains separate. However, at the 6.6 mm stage (fig. 65 E), it has fused, in its posterior part, with Meckel's cartilage. In the course of its further development, it more and more invades the cartilage in the posterior part of the mandible. Apart from this bone only one additional bone forms in this part of the cartilage, viz. the retroarticular (*ra.*). The latter is situated in the ventro-caudal part of the mandible, at the place of attachment of a strong ligament from the suboperculum. Just as in *Phoxinus*, there are, thus, only two ossifications in the posterior part of Meckel's cartilage, viz. the retro-articular and angular ones.

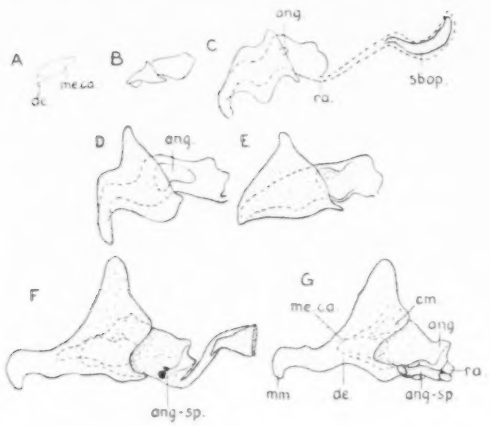

Fig. 65. *Nemachilus barbatula*. Development of lower jaw. A: 4.0 mm, 50 ×. B: 4.3 mm, 50 ×. C: 5.5 mm, 50 ×. D: 6.0 mm, 60 ×. E: 6.6 mm, 30 ×. F: 33 mm, 16 ×. G: 70 mm, 16 ×.

Also, an articular bone is missing here. Apart from these bones, there appears a further one, formed comparatively late, dorsally to the middle part of the cartilage. This is identical with the above described corono-meckelian bone (*cm*). In this fish, however, this bone is, from the beginning, independent of the cartilage and remains so the whole time. The latero-sensory component forms only at a comparatively late stage. As previously mentioned, this fish lacks a mandibular canal. As a result, no canal bones will appear within this region. In the absence of the dental-splenial bones, the dental in this fish is only a mento-mandibular-dental bone. On the other hand, a short canal forms in the angular region and, in connection with the neuromast that is to be found in this canal, a single bone (fig. 65 F) appears, at the 33 mm stage. This bone primordium gradually develops into a cylindrical bone round the canal (fig. 65 G). This bone does not fuse with the underlying bone, but will all the time remain separate. This bone is an angular-splenial one (*ang-sp.*). At the 33 mm stage (fig. 59) another latero-sensory bone primordium is to be found, situated exactly between the posterior edge of the mandible and the anterior edge of the preoperculum. In a 47 mm long specimen, this primordium has developed into a cylindrical bone round the canal. In the examined 70 mm long specimen this bone is lacking. It lies freely in the epidermis, without any underlying bone. Whether it should be regarded as belonging to the angular bone or to the preoperculum, I am not in a position to state.

The preoperculum. The first primordium of this bone appears at the 5.5 mm stage, in the shape of a single blastema, in connection with two or, possibly, three neuromasts (fig. 66 A). As in the case of the previously examined fishes, it is, also here, difficult to distinguish between the neuromasts, since, very early,

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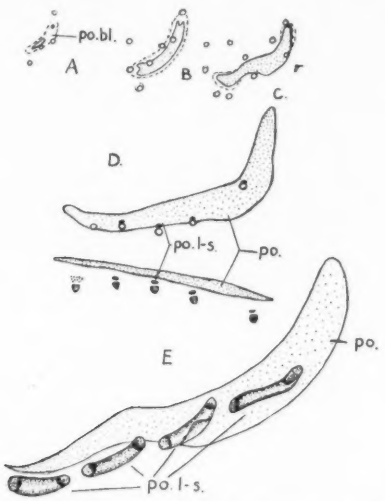

Fig. 66. *Nemachilus barbatula.* Development of preopercular bone. A: 5.5 mm, 50 ×. B: 6.0 mm, 60 ×. C: 6.6 mm, 60 ×. D: 33 mm, 16 ×. E: 70 mm, 16 ×.

a considerable number of secondary organs has been added. In connection with one of the organs, a small bone primordium has formed in the blastema. In a slightly older specimen (fig. 66 B) both the blastema and the bone have grown markedly. The bone has begun to assume its characteristic sickle shape. In spite of the fact that the blastema forms in connection with several organs, probably four or five, only one bone primordium appears, which, later, will extend below the other organs. In a 6.6 mm long specimen, the bone has grown further, and the blastema remains only in the anterior and posterior parts of the bone (fig. 66 C). At the 33 mm stage, the latero-sensory component begins to form, in connection with five of the primary preopercular neuromasts. Below the foremost of these organs, there is, as yet, only one single blastema (fig. 66 D), while a bone has formed beneath the other four. Like the blastema, this bone is single, in contrast with the conditions in the previously examined fishes, in which the corresponding earliest bone primordia are distinctly binary (cp. *Phoxinus,* fig. 56 B). In the adult specimen, these bone primordia have grown into tube-like bones round the canal, which have neither fused with one another, nor with the underlying lamellar part of the preoperculum (figs. 60, 66 E).

On account of the comparative shortness of the preopercular canal in this fish, the suprapreopercular bones are absent.

Bones formed in connection with the temporal canal.

As previously stated, the supratemporo-intertemporal bone in *Phoxinus* consists of three genetically different bones that, later, fuse into one unified bone.

In *Nemachilus*, this bone has a partly different structure. In this fish the membranous component is missing, and the canal component does not fuse with the underlying bone. The cartilage-bone component, the opisthotic, forms in this fish comparatively early, with approximately the same position and extent as in *Phoxinus*. On the other hand, a membrano-pterotic bone is lacking. At the 21 mm stage, the latero-sensory component appears as three small bones, two connected with the intertemporal organs, one with the supratemporal organ. When the canal invaginates, they will form as cylindrical bones, as normal to this fish. These three canal bones do not fuse either with one another or with the underlying cartilage-bone (fig. 59, *it., st.*). In the adult (fig. 60, *st.*) the bones retain the same appearance. The supratemporal bone is closely joined with the extrascapular-lateral bone (*es.l.*).

Bones formed in connection with the supratemporal commissure.

In connection with this canal, two canal bones form, viz. an extrascapular-medial and a lateral one (*es.m., es.l.*). The former of these bones fuses, secondarily, with the posterior part of the parietal bone, while the latter, as previously described, fuses with the supratemporal bone. Also these bones lack a lamellar component.

7. THE CANAL BONES IN *COBITIS TENIA* L.

(Fig. 67.)

As previously stated, this fish lacks canals. Also in the adult, the neuromasts remain in the epidermis, and no signs of any canal invagination can be detected. As a result, this fish is completely without any latero-sensory components. Only the lamellar component is left of the so-called canal bones.

Thus, the nasal bone is missing in the supraorbital row of bones. Only the lamellar part of the frontal bone (*fr.*) is to be seen. This is quite normally developed and covers the dorsal side of the orbito-temporal region.

In the infraorbital row, there is only a small rod-shaped antorbital bone (*ao.*) left, immediately in front of the markedly developed, movable ectethmoid bone (*ecm.*). There are no infraorbital bones.

In the mandibulo-preopercular row of bones, the splenial bones are absent. Thus, this fish, like *Nemachilus barbatula*, has but an os dentale-mento-mandibulare (*de.*). Only the lamellar part of the preoperculum can be seen (*po.*). As compared to the above described fishes, it is rather feebly developed, consisting of a narrow bone, of a uniform breadth.

Also the intertemporo-supratemporal bone is lacking. An opisthoticum ossifies in the cranial wall, but, as in *N. barbatula*, a membranous component is

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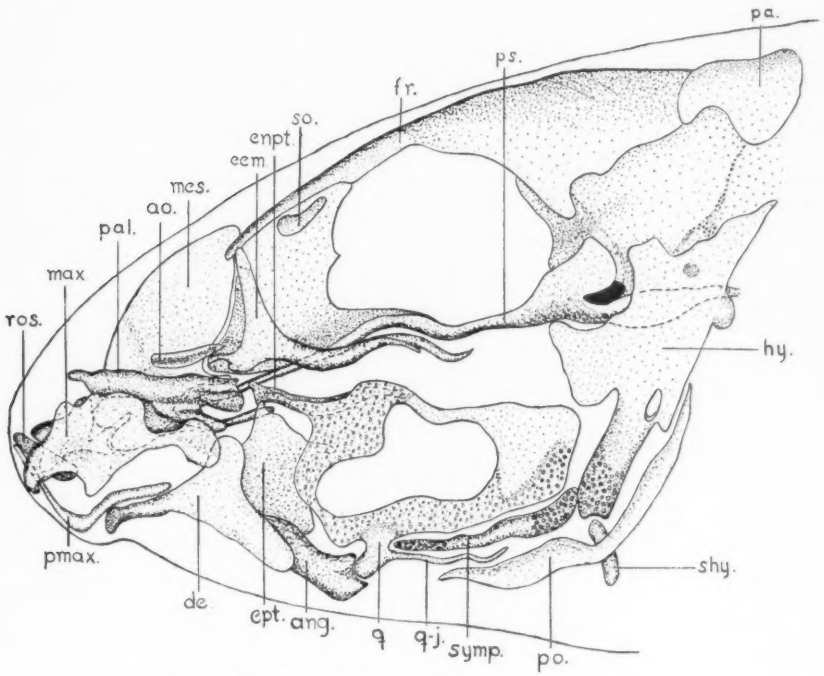

Fig. 67. *Cobitis taenia*, 38 mm. Anterior part of skull. 16 ×.

lacking. Only the cartilage-bone component is left of the three different components that form this bone in *Phoxinus*.

There are no extrascapular bones.

V. SUMMARY OF VIEWS ON THE VARIOUS CANAL BONES.

The nasal bone. In all the examined fishes, the nasal bone, when present, consists exclusively of the latero-sensory component. Throughout, the lamellar part is missing. This was reported also by SAGEMEHL (1891), who stated that this bone in the Cyprinids is, without exception, very small, in contrast with the conditions in the Characinids, which have a well developed nasal bone with a lamellar component. In the Silurids, the conditions vary. Different types occur. In *Corydoras*, which lack canals, also the bone in question is missing. In *Chrysichtys nigrodigitatus*, only the latero-sensory part exists, but in, e.g., *Clarias*, the bone is composed, in addition, of a well developed lamellar component. The same applies to *Ameiurus* (KINDRED 1919). In this fish, to begin with, a tube-like bone forms, which later fuses with an underlying membranous

bone, that has formed in the connective tissue. It is to be regretted that KINDRED fails to provide any details regarding the process of formation of this membranous bone. In the Homalopterids (RAMASWAMI 1948), which, from a systematic point of view, should, probably, be placed between the Cyprinids and the Cobitids, the nasal bone consists, likewise, only of a tubal bone.

As has appeared from the previous description, the nasal bone does not form in the same way in the examined species. Thus, at first, two or three separate bones form, which, later, will either fuse with one another or remain free. Also in other fishes the nasal bone will, to begin with, form in different parts. In *Amia* (PEHRSON 1922, 1940) and in *Lepidosteus* (HAMMARBERG 1937) three bones form and fuse. In *Esox* (PEHRSON 1944 a), on the other hand, only one nasal bone appears. In a great many more primitive fishes, a row of independent nasal bones is a common feature, e.g., in *Osteolepis* (JARVIK 1948), to mention only one instance. In the great majority of examined recent Teleosts, there is, as a rule, only one nasal bone, but the embryological development shows that, from the beginning, several separate elements may form. In all likelihood, these free nasal primordia represent the separate nasal bones in more primitive fishes, though, in now living fishes, they have, generally fused into one bone.

In the examined fishes the nasal bone originates, without exception, in single primordia. In some other examined fishes, on the other hand, binary primordia are at first formed. In, e.g., *Amia* (PEHRSON 1922, 1940) binary blastemas and paired bone primordia form. In *Esox* and *Salmo salvelinus* (PEHRSON 1944 a) single blastemas, but binary bones, appear, and in *Salmo salar* single blastemas and bones with an indication of a binary origin in the posterior part.

The frontal bone. In fishes, this bone forms in an extremely variable manner. Even in such fishes as are rather closely related, as those examined above, there are several types of formation, with regard to both the lamellar and the latero-sensory part of the bone.

In *Nemachilus,* the lamellar part originates in a blastema with some relationship to the supraorbital neuromasts. In this blastema the lamellar part forms, in the shape of three separate bone elements, each connected with a neuromast of its own. Soon the different bone lamellae will fuse with one another. A similar type of formation of the lamellar part of the frontal bone has been described by PEHRSON (1944 a) in *Esox.* Also in that fish, this part forms in a blastema that appears in connection with three supraorbital neuromasts. In this blastema three bones, that later fuse, form. As to the mode of formation PEHRSON writes as follows: "... the bone has its origin from the sense organs in the future canal." A similar type of formation is to be found in *Salmo irideus* (DEVILLERS 1944 a).

In *Leuciscus* and *Phoxinus,* on the other hand, this bone is formed in a different way. In these fishes, there is no perceptible blastema. The bone forms

in an irregular manner in the subcutaneous connective tissue. The neuromasts do not seem to have any influence on the bone formation in these species.

Also the latero-sensory component forms in different ways, the connection with the lamellar part differing from one species to another. In *Amia,* a cylindrical bone will first form round the canal, as it invaginates, and, later, lamellae will grow out from this bone. In all so far examined Teleosts, the lamellar part will first appear, followed, sooner or later, by the latero-sensory part. From the beginning, these two components may be mutually united. This applies, e.g., to *Leuciscus, Esox* and others. The latero-sensory portion then grows from the lamellar part. In *Phoxinus* and *Tinca* these parts form independently but fuse later, with a final result similar to that in the first-mentioned fishes, irrespectively of the differences in the development. Finally, in *Nemachilus,* the two parts never fuse with one another. In the species analysed in this investigation, the latero-sensory part forms, without exception, as single primordia. The primordia of *Amia, Esox* and *Salmo irideus,* on the other hand, are binary.

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The following two typological series of the development of the bone can be set forth: one showing the development of the lamellar part, the other the relationship of the lamellar and the latero-sensory component.

With regard to the first-mentioned series, in the Teleosts the lamellar part forms from a blastema in which the first bone primordia appear in a direct connection with the neuromasts. At the next stage, a blastema is, likewise, found, but the first bone primordia do not arise in the same close connection with the organs that appear earlier, and, finally, no blastema is detectable. The blastemas and the bones form, at first, in an irregular manner in the subcutaneous connective tissue, without any noteworthy relationship to the neuromasts, a type of formation that resembles that of bones that do not contain any canals.

As to the other series, the two components may be found to be closely united with one another, at first, and then to develop separately, either fusing or remaining independent. Finally, there are fishes without canals, in which, at the ultimate stage, only the lamellar part is left.

When these two typological series, which in the above-mentioned fishes appear independently of one another, are compared, an originally typical canal bone will be found to form and develop as a normal dermal bone, without any canal component, or, in other words, like a frontal bone of a tetrapodous type.

Latero-sensory supraorbital elements in the parietal bone. As the previous description has shown, the supraorbital canal, in *Leuciscus, Alburnus, Abramis* and *Tinca,* extends out on the anterior half of the parietal bone. In connection with the neuromasts in this canal, canal bones form that may either, from the beginning, be united with the parietal bone or, secondarily, fuse with it. Morphologically, they have nothing in common with the parietal bone, but have

developed, secondarily, in connection with that bone in the same way as the extrascapular bones. This is, moreover, obvious from the fact that these bones fuse with the parietal and not with the frontal bone. This applies particularly to *Phoxinus*, but also to *Nemachilus*, in which the canal is similarly prolonged but ending on the frontal bone. A schematic illustration of this will be found in fig. 41. It seems to me superfluous to construct a particular term for these bony elements in the parietal bone since, in my opinion, they are latero-sensory supraorbital elements that, owing to the prolongation of the canal out on the parietal bone, have happened to fuse, secondarily, with these bones, instead of amalgamating with the frontal bone.

The antorbital bone. In all the examined Cyprinids, the antorbital is a large bone, covering the side of the nose. In all the analysed fishes the bone has a uniform appearance. In *Nemachilus*, on the other hand, the bone is longitudinal and rather narrow, owing to the comparative length of the nose in that fish. Like the frontal bone, it consists of two components, that differ considerably as regards the time of their respective formation. Unlike the frontal bone, however, this bone, in all the examined species, forms as a blastema in connection with the foremost neuromasts in the infraorbital line. A great many organs appear to be engaged in the formation of the blastema but, nevertheless, a bone arises that is from the first single. The latero-sensory component, that forms considerably later, consists, on the other hand, of a bone primordium connected with each of the participating neuromasts. Also with regard to this bone, the same relationship, between the lamellar and the canal component, as in the frontal bone is observed. Either the components are united from the first, or they form separately, to fuse secondarily. In the Homalopterid *Bhavania* (RAMASWAMI 1948), the canal component in the antorbital bone remains separate. In fishes that lack a canal, only the lamellar portion develops.

In all the earlier examined Ganoids and Teleosts, the first primordia of the bones have, without exception, been single. This also applies to the fishes analysed by me, with one exception, viz. *Nemachilus*, in which the primordia of the latero-sensory bones are binary (fig. 64 C).

In *Amia* (PEHRSON 1922, 1940), the bone forms from the organs 3—6 in the infraorbital line. In the opinion of PEHRSON, all the neuromasts concerned in this instance would belong to the infraorbital series. According to WESTOLL (1937), on the other hand, the organs 3 and 4 would pertain to the rostral commissure. From this contention he draws the conclusion that the antorbital bone would consist of rostral, as well as of antorbital, elements. This has been denied by PEHRSON (1940). It is, he presumes, hardly probable that an originally single blastema would be derived from organs in two diffrent canal portions. For the sake of comparison, he mentions the formation of the complex intertemporo-supratemporal bone, which forms in connection with three organs, innervated by two different nerves. This bone originates in different primordia

which later fuse. In that case the separate formation of the bones depends on the different innervation of the neuromasts. In the antorbital region, both organs in the rostral commissure and the infraorbital canal are innervated by one and the same nerve. For this reason a uniform formation of the blastemas is not inconceivable.

As previously stated, with regard to the lateralis system, the infraorbital line curves, in its anterior part, towards the dorsal side, in the direction of the posterior nasal opening. In the course of the further development, the upward part directed dorsad will belong to the antorbital line, while the rest of the organs will lie in the infraorbital canal. The dorsal canal branch in *Amia*, lodging the organ 5, is, probably, homologous with the antorbital line in the Cyprinids. If so, the infraorbital canal in *Amia* would begin with the organ 5, and the organs 3 and 4 would belong to the rostral commissure. This would support WESTOLL's suggestion that also rostral elements are likely to form part of the antorbital bone in this fish.

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From the conditions in *Esox* (PEHRSON 1944 a) and *Clupea pilchardus* (WOHLFAHRT 1937), quite apart from what has been previously stated above, regarding *Phoxinus*, it is obvious that blastemas form also from the antorbital pit-line. In *Esox*, the rostral bone arises in a slightly different way, in so far as four primary antorbital bones appear, which are later to fuse with one another. One of these bones forms in connection with an organ belonging to the antorbital line. In *Clupea*, the antorbital line is invaginated in a canal, and one of the organs in this canal portion lies in the antorbital bone. In this connection, it should be pointed out that the antorbital part of the canal continues in an additional bone, dorsally to the antorbital bone, i.e. the "supraorbitale 2". In this bone one organ lies. However, according to WOHLFAHRT, this would not be a canal bone. This suggestion of his is questionable, but, until properly examined, the question has to be left open.

In sum, the lamellar part of the antorbital bone in the examined fishes may be said to originate from a complex blastema, formed in connection with several neuromasts belonging to the infraorbital, as well as the antorbital line, while the latero-sensory component is derived exclusively from the infraorbital organs.

The infraorbital bones. In the previous description, no distinction has been made between lachrymal, infra- and postorbital bones. All the bones have been termed infraorbital, a homologisation of these bones proving difficult, because of the marked variations in the number of the bones from one species to another, and the fact that the number of bones may differ even from one side to the other in one and the same specimen.

In the examined Cyprinids, the infraorbital bones form in the same way as the antorbital bone, i.e. a complex blastema, in which the bone arises without any signs of a serial formation, appears first in connection with the infra-

orbital neuromasts. Then, a latero-sensory component is added, serially. In *Nemachilus,* only the latter component is to be found, and, since the different bones do not fuse, many infraorbital bones appear in this fish. In *Cobitis taenia, Corydoras,* and other fishes that lack an infraorbital canal, also the infraorbital bones are missing. In all the examined fishes these bones form from single primordia, with only one exception, viz. *Nemachilus,* the first infraorbital bone of which appears from a binary bone primordia. The second bone shows signs of a binary origin, while the others form from single primordia, as in other fishes.

The supraorbital bones. In spite of the fact that these bones are not canal bones, they should, in my opinion, justify a short mention in this connection. In the Teleosts, these bones are markedly variable, sometimes being absent, sometimes appearing in different numbers. This variability is conspicuous in the fishes examined here. In spite of their rather close relationship, the variations are pronounced. Thus, *Phoxinus, Alburnus* and *Abramis* have one bone, *Leuciscus* and *Tinca* two. *Among* the Cobitids, *Cobitis taenia* has one, while *Nemachilus* lacks the supraorbital bone. The bones form comparatively late, in *Phoxinus,* e.g., only at a length of 23 mm, in the subcutaneous connective tissue, without any relations to the neuromasts on the dorsal side.

The splenial bones. The account of *Phoxinus,* where these bones were comprehensively dealt with (p. 81), should be referred to.

The preoperculum. Fundamentally, this bone forms in the same manner as the antorbital bone. A blastema appears, immediately underneath the sense organs in the preopercular line. Several organs participate in its formation. A single bone is formed from the beginning. No indication of a binary or serial origin can be traced. Far later during the development, the latero-sensory component forms, likewise in a direct contact with the sense organs. However, these bones form serially, one in connection with each neuromast. In the analysed Cyprinids, the primordia of these bones are binary, while, in *Nemachilus,* they are single. Also as far as this bone is concerned, the two components may either, from the beginning, be fused with one another, as in *Leuciscus,* or form separately, to join only later, as in *Phoxinus* and *Tinca,* or remain separate, as in *Nemachilus.* In *Cobitis,* the latero-sensory part is missing.

The suprapreoperculum. Since the preopercular canal in the examined fishes without exception is comparatively short, never reaching up to the temporal canal, this bone is seldom developed. Only in *Alburnus* there is a canal bone that can be properly so called, secondarily fused with the operculum. In *Leuciscus,* DEVILLERS (1947), has made the same observations. Personally, I have not noticed any such bone in my material, possibly because of the fact that I have not examined sufficiently old specimens. On the whole, this bone is comparatively rare in the Teleosts. HOLMGREN—STENSIÖ (1936) mention only *Salmo, Cottus, Anguilla* and *Amiurus.* In *Alburnus* and *Anguilla* which

I have been in a position to study, this bone is a latero-sensory one without any membranous components. In fishes with a short lamellar preoperculum these canal components become free, in the shape of suprapreopercular bones, provided they do not secondarily fuse with the underlying operculum, as in *Alburnus* and *Leuciscus*. Thus, these bones constitute an independent continuation of the latero-sensory parts in the preoperculum. The degree to which the lamellar part of this bone extends towards the dorsal side decides whether the latero-sensory components are to be free or not.

The pteroticum. As previously stated, this bone consists of a number of elements formed in different ways. The composition of the bone varies from one species to another. Among the components in all the here examined Cyprinids, there is, without exception, a cartilage-bone that forms, in the cartilage laterally to the horizontal semicircular canal and is rather to be regarded as an opisthoticum (HOLMGREN—STENSIÖ 1936). Laterally to this bone, a dermal bone, the "membrano-pterotique", acc. DEVILLERS (1947), forms in the connective tissue, without any noteworthy relationship to the neuromasts that lie outside it. This bone may either form independently of the underlying cartilage-bone (*Phoxinus*) or be closely united with it from the beginning (*Leuciscus*). In *Nemachilus* and *Cobitis*, the membrane bone is missing.

In *Salmo irideus* (DEVILLERS 1947) and *Esox* (PEHRSON 1944 a), this membranous component forms in a slightly different way, in so far as it develops from blastemas that have formed in connection with the temporal neuromasts. In the first-mentioned fish two blastemas appear, in the latter only one. In this blastema, the bone arises that later fuses with the underlying opisthoticum.

To these two components yet another is added, viz. the latero-sensory, which in the examined Cyprinids consists of three bones, two intertemporal and one supratemporal. *Tinca* has a larger number of canal bones. They may have the same relationship to the underlying bone as previously described with regard to the frontal bone. In *Cobitis taenia* also the latero-sensory component is absent and, consequently, this fish lacks a pteroticum. Summarising, the pteroticum in the Cyprinids may be said to consist of an intertemporo-supratemporo-membranopteroticum-opisthoticum. In this connection, it should be mentioned that PEHRSON (1944 a), adopts a somewhat different nomenclature, in so far as he applies the term pteroticum to the cartilage-bone that has here been called the opisthoticum. The nomenclature preferred by the present author has, however, been generally employed, and is used by HOLMGREN—STENSIÖ (1936), among others.

Also as far as the pteroticum is concerned, a typological series of development can be observed in fishes with an intertemporal and a supratemporal bone, e.g., certain Crossopterygii (JARVIK 1948, and others), these bones being, probably, genuine canal bones. Later, these bones fuse with one another into a single

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bone, e.g., in *Amia*, where the whole bone is, likewise, a canal bone. In the course of the further development, the lamellar part of the bone gradually ceases to be dependent on the neuromasts, sinking deeper into the underlying tissues, finally losing its contact with the neuromasts, becoming, instead, more dependent on the underlying cartilage with its perichondrium. Alongside of this course of development, the canal component releases itself more and more, being, after a time, completely free or even disappearing.

VI. DISCUSSION.

In the preceding chapters an account has been given of the sensory line system and the canal bones in some Cyprinids, Cobitids and Silurids, comprising details of the conditions in the adult fishes, as well as of the formation and development of the system and bones in some species.

From this it has been obvious that the lateral line system in the Cyprinids is, on the whole, markedly uniform, in spite of fairly pronounced variations in specific details. In several respects, the Silurids differ from this "Cyprinid pattern". Thus, the Silurids have only one sense organ innervated by the otic nerve. They lack a supratemporal commissure and, without exception, have comparatively few pit-lines. As far as the Cobitids are concerned, the examined species are too few to justify the attribution of any special characteristics to this family. However, the examined *Nemachilus barbatula* disagrees in various particulars from the forementioned families, inter alia in the order in which the canals invaginate, as well as with regard to the early formation of certain pit-lines, etc. The fully developed system rather resembles that of the Cyprinids than that of the Silurids.

As to the Cyprinids, it is interesting to note that, in the three species of which the present author has had an opportunity to study early stages, the system at a certain point of development, viz. when the primary neuromasts differentiate from the placodes, is practically identical (*Leuciscus* fig. 8, *Phoxinus* fig. 14 and *Alburnus* fig. 23). A corresponding early stage of *Nemachilus*, on the other hand, is different, since certain pit-lines in that fish form very early, as compared to the other fishes. From this common initial stage, the sensory line system in the Cyprinids develops in somewhat different directions, resulting, finally in variations in appearance in the adults. A common pattern can, in spite of this, be clearly noticed also in the adults. One characteristic of all the analysed species is an extremely well developed line system, with lines common to all these fishes, differing, it is true, somewhat in aspect and extent but, nevertheless, well comparable. Other distinctive traits are, to judge from reports in the literature, the late formation of the canals, their mode and order of formation and their position and extent on the head.

The pit-line system.

As shown above, the pit-line system is, in particular, amply developed. From an embryological point of view the free neuromasts are not all of an equal significance. Thus, some have developed directly from the placodes, i.e. primary neuromasts. Later, the majority of these will be incorporated in the canals as canal organs, while some of them will always be left in the epidermis and form part of pit-lines. These "primary pit-lines" may, as pointed out above, in the more primitive Actinopterygii, correspond to canals. This applies, for instance, to the rostral pit-commissure, which in *Elops, Clupea, Amia, Polypterus,* and others, correspond to an ethmoidal canal. The same applies to the antorbital line which, similarly, at least in *Clupea* and *Amia,* corresponds to a canal. To this category of lines, the anterior mandibular and the nasal line belong. They constitute a direct continuation of the mandibular and supraorbital canals, respectively. Everything seems to suggest that the anterior organ or organs in these lines have not been invaginated in canals but left in the surface. As previously mentioned, such primary, uninvaginated neuromasts disclose a marked tendency to increase in number. This is especially conspicuous in the Gobiids, a matter to which I hope to return in a future investigation.

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The rostral pit-commissure and the antorbital line, both develop from a common placode and, in all the examined specimens, they are innervated by one and the same branch of the n. buccalis which, in addition, innervates also one or two organs in the anterior part of the infraorbital canal. In, e.g., *Phoxinus,* only the foremost organ in the canal is innervated by this nerve. It is the only organ in this canal that, apparently, does not participate in the formation of the lamellar part of the antorbital bone (fig. 16). The organ pertains to either of the two forementioned lines and, to judge from the conditions in *Esox* (Pehrson 1944 a), it seems likely to belong to the antorbital line. Observations in *Clupea pilchardus* (Wohlfahrt 1937), lead to the same conclusion, since the anterior part of the infraorbital canal in this fish curves sharply dorso-caudad, towards the bridge between the nose and the eye. According to Wohlfahrt, the organs in this part of the infraorbital canal do not participate in the formation of the underlying canal bone. In *Nemachilus* the antorbital line has a slightly different appearance, in so far as it is parallel to the infraorbital canal. This is explained by a lenghtening of the nose through a marked, comparatively late growth. In the course of this process the line is carried rostrad, thus obtaining a position characteristic to this fish.

Another type of pit-lines forms through a "budding" from the primary neuromasts. Unfortunately, this is not always easy to ascertain, since the process often passes comparatively rapidly. In order to secure actual proofs, examinations of stages, very close to one another, would be required. The formation of these lines mostly occurs when the fishes have become fairly large,

and it is difficult, then, to obtain the suitable stages, considering, particularly, that the length of the fish often fails to correspond to its stage of development. In certain instances, this type of formation has been definitely proved. In other cases, the process is more uncertain and, to be conclusively established, further examinations would be necessary. As far as the lateral supraorbital line, as well as the opercular lines, are concerned, this origin has been demonstrated. The same applies to the accessory infraorbital line, as well as to the corresponding preopercular line, and, finally, also to the medial extrascapular line. It is, on the other hand, uncertain whether the free organs that are innervated by the otic and the glossopharyngeal nerves actually derive from the organs of the temporal line. In these fishes the canals are, without exception, accompanied by those parallel lines that often lie laterally to the canals. Thus, the supraorbital canal is escorted by the anterior part of the lateral supraorbital line and, partly, also by the nasal line, the infraorbital canal by an accessory line, the preopercular canal by a similar line, the temporal canal by a number of free organs and the upper part of the supratemporal commissure by the extrascapular line. From a number of fossil Crossopterygii, viz. *Osteolepis*, *Eustenopteron* and *Holoptychius*, JARVIK (1947) reproduced the same observation, viz. that certain canals are accompanied by pit-lines. Further, PEHRSON (1944 a), found a differentiation of certain parts of the infraorbital line in the canal neuromasts and pit-lines of *Esox*. In *Nemachilus*, the accessory preopercular line forms through a differentiation of a preopercular line, seemingly single from the beginning, but as far as the other fishes are concerned, these lines form by means of a "budding". Here, then, two types of formation present themselves, but, in principle, the difference between these two types is, probably, inconsiderable.

Further, the upper part of the preopercular canal is often accompanied by a parallel line, but this line has formed in a different way, and its position depends, actually, on the fact that the distance between the eye and the preopercular canal in these fishes is very short, a circumstance that, so to say, has caused the lines to be pressed together. In fishes with long cheeks, e.g., *Anguilla*, the distance between this very vertical line and the canal is considerable. In sum, it can be stated that, in the Cyprinids and, to judge from the literature, in many other fishes, the primary lines posses a capacity of duplication.

Finally, there is in the examined fishes a third type of pit-lines. Whether they actually differ in their mode of formation from the others, is difficult to say, but in all examined fishes I have made the same observation. These lines neither appear from placodes, nor are they being detached from primary lines. The organs come suddenly into view, sometimes far from any primary neuromasts and not from any noticeable placodes. In the Cyprinids, such lines are the horizontal and the vertical line on the cheek, the medial supraorbital line and

the symphysial line. Since data regarding the formation and development of these lines in other fishes are very sparse or entirely missing, they will, for the time being, have to be regarded as a type of their own. Examinations of some other fishes, in which the conditions may, perhaps, prove to be different, will provide a difinite answer to questions regarding their origin and actual nature.

Among these lines, the horizontal and the vertical line on the cheek attract particular interest. In none of the analysed Cyprinids has it been possible to observe the earliest development of these lines. As to *Leuciscus*, I have been in a position to examine a large number of closely adjoining stages, and in young specimens, up to 11—12 mm, I have discovered no sign of these lines, whether in the shape of placodes or organs. In 13—14 mm long specimens, on the other hand, organs have suddenly formed, approximately along the whole length of the definite line. Roughly, the same takes place also in *Phoxinus* and *Alburnus*. In *Nemachilus*, the conditions are slightly different. In contrast with the abovementioned fishes, these lines form in *Nemachilus* very early, i.e., at the 3.4 mm stage (fig. 30). At such young stages the picture of the lines in question differs from that in the adult. For this reason, these lines are particularly interesting. They render an interpretation of their actual identity possible. The late formation of these lines in the other examined species has not allowed any interpretation. The observations in *Nemachilus*, in this respect, should justify conclusions also regarding the earlier stages of development in those fishes. I am indebted to Professor N. HOLMGREN for having suggested this to me.

The horiontal line, i.e. the supramaxillary line acc. STENSIÖ (1947), connects the preopercular and infraorbital lines. STENSIÖ distinguishes in the supramaxillary line an anterior, a middle and a posterior part, varying in appearance from one fish to another. At an early stage in the development of *Nemachilus* (fig. 30), the preopercular line curves rostrad towards the posterior part of the infraorbital line. The upper part of this line constitutes the horizontal pit-line. During the subsequent development, it will detach itself from the preopercular line and more and more change its orientation till, in the adult, it will lie vertically, side by side and in front of the upper part of the preopercular line. Thus, the horizontal line is, when fully developed, destined to occupy a vertical position. Through its position and innervation this line has been definitely shown to be homologous with a far longer vertical line which is to be found in all the examined Cyprinids, extending, in those fishes, along the main portion of the vertical part of the preopercular canal.

The vertical pit-line, i.e., acc. STENSIÖ, the postmaxillary line, forms, according to that author, as a ventral branch of the anterior end of the middle part of the supramaxillary line. The same author also states that the oral line develops as a direct continuation of the vertical line. In the Actinopterygii, in which the middle part of the supramaxillary line is short or absent, it grows out immediately in front of the preopercular line. During the young stages of

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Nemachilus, there is, on the cheek between the infraorbital and preopercular line, a further line which issues from the horizontal line, extending rostrad parallel to the infraorbital and preopercular lines. As previously shown, this line reaches to the quadrato-mandibulary joint, where it directly continues in an oral line on the mandible (figs. 32, 33). Thus, it agrees extremely well, in course and extent, with STENSIÖ's postmaxillary line. In its further development this line loses its contact with the oral line. In older specimens (fig. 36), it extends from the upper part of the preopercular canal in a horizontal direction towards the nose. In all the examined fishes this line is particularly well developed, often, like a pit-field, covering the whole region between the mandibulo-preopercular and the infraorbital canals. Accordingly, the development in *Nemachilus* shows that, from an embryological point of view, the horizontal line on the cheek in the adult is identical with the vertical pit-line and, vice versa, the vertical line with the horizontal. The conditions in the Cyprinids must, to judge from all indications, be indentical, in spite of the fact that the embryological development cannot, in that instance, be observed in the same way. As STENSIÖ did not know the ontogeny, he has based his interpretation of the lines in *Phoxinus* (1947, fig. 21 A) on the conditions in the adult and arrived at an erroneous conclusion. STENSIÖ's hc_1 should, therefore, be identical with the vertical line, hc_2 with the upper part of the horizontal line, while, finally, hc_3 is a line difficult to interpret. From the innervation it is evident that this group of organs is innervated partly by the n. oticus, partly by a branch of the n. opercularis superficialis. In the descriptive chapter above, I have called this group "the suprapreopercular line", in accordance with the conditions in the Gobiids and *Anguilla*, but as to the interpretation of this line, I have at present no opinion. Further, STENSIÖ's "postmaxillary line" (orp) is identical with the horizontal pit-line and the posterior part of the oral line (orp_1) with the accessory preopercular line, while, in my opinion, the anterior part of the same line is an anterior mandibular line, forming a direct continuation of the mandibular line.

In, e.g., *Amia*, the horizontal line runs from the preopercular canal horizontally towards the infraorbital canal, on a level with the eye, while the vertical line isues from the ventral side of this line. How, then, is this peculiar feature in the Cyprinids to be explained? Supposing that the two forementioned lines in *Amia* were to rotate 45°, the horizontal line thus becoming vertical, and vice versa, a position characteristic of the Cyprinids would be obtained. Is it, then, possible that, in the course of the development, such a rotation has taken place? Undoubtedly, this has happened, and precisely in connnection with the growth of the mandible. In the youngest specimens of the *Nemachilus*, the anterior edge of the mandible lies just below the eye. It is, then, possible to follow its gradual growth rostrad. Thus, at the 4.3 mm stage, it is situated on a level with the anterior edge of the eye. From there it moves more

and more rostrad, while, at the same time, the nasal part of the head markedly lengthens. Change in the position of the mandible, combined with the lengthening of the nose, causes a general movement rostrad also of the sense organs. This is particularly accentuated on the lateral and ventral sides of the head. This process is obvious from the opercular organs which, at the 3.4 and 4 mm stages (figs. 30, 31), are placed one straight below the other. Already at the 4.3 mm stage (fig. 32), the mutual position between these organs has changed, the line now lying obliquely, with its lower part moved rostrad. At more advanced stages, this oblique direction becomes increasingly marked. At the 5.3 mm stage (fig. 34), the organs occupy an almost horizontal position, the foremost projecting below the preopercular line. From this it emerges that a marked change actually takes place, a fact that may explain the alterations in the orientation of the horizontal and vertical lines. Also in the other examined species a similar movement can be traced, even though less conspicuous there than in *Nemachilus*. From the illustrations published regarding the development in *Amia* (ALLIS 1889, PEHRSON 1922, 1940), no changes would seem to have occurred. Thus, the lines in this fish have retained their original orientation.

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In connection with the pit-line system, I should like to call attention to the ampullae of Lorenzini in the above described Silurid *Plotosus anguillaris*. From the description above, it was evident that this fish had a completely normal canal system, while lacking free neuromasts. Instead, it has a well developed ampullar system, built after the same pattern as in *Selachia*. Further, it is well provided with terminal buds. In these circumstances, the first suggestion that offers itself is that the pit-lines have been replaced by, or changed into, an ampullar system or, in other words, that free neuromasts and pit-lines may be homologous with these ampullae or ampullar groups of Lorenzini. Earlier, several authors have tried to homologize the ampullae with the so-called nerve sacs in the bone ganoids. According to this, the ampullae and nerve sacs would be organs without any homologue in other fishes. In his work on *Mustelus*, ALLIS (1901) suggests the possibility that the ampullae and nerve sacs correspond to the "surface sense organs" in *Amia*. He says: "The terminal buds of Ganoids, the nerve sacs of Acipenser and the ampullae of Selachians are in all probability homologous structures." ALLIS made an attempt to prove this idea, inter alia, by pointing out that the majority of the pit-organs in *Amia* are homologous with the canal organs in *Mustelus*. For this reason, the ampullae could not correspond to anything else in *Amia* and the Teleosts than the end buds. In this connection, he mentioned the absence of such buds in *Mustelus*. Moreover, he attempted to show that the innervation centre of the ampullae was different from that of the lateralis lines. JOHNSTON (1902) submitted ALLIS' fore-cited statements to a detailed examination. His conclusion was that none of the arguments propounded by ALLIS were in any way convincing. In particular, he rejected ALLIS' statements with regard to the innervation. Not-

withstanding JOHNSTON's criticisms of ALLIS' conception, RUUD (1920) was of the opinion that ALLIS may, nevertheless, be right. She mentions the following similarities between the terminal buds in *Amia* and the ampullae in *Spinax:* "they appear in groups from thickened ectodermal fields, being first seen as fine whitish spots adjoining a canal line". They form later than the lateral line primordia and have approximately the same distribution on the head in the two fishes. However, the greatest obstacle to a homologization meets in the innervation. HERRICK (1899), makes the following statement regarding the innervation of the terminal buds: "The communis system is represented in the VII, IX and X nerves. The terminal nucleus for all of its fibres lies in the lobus vagi. This system is very completely isolated and unified in the head, and yet is apparently related to a sensory system of the trunk, closely associated with the spinal viscero-motor centres (intermediate zone). The communis system was primarily a viscero-sensory (entodermal) mechanism. — — — In its cranial portion it also supplies taste buds and terminal buds (ectodermal organs)." With reference to these quotations, and to JOHNSTON's forementioned criticism, a homologization of the ampullae and the terminal buds seems to be out of the question. Since, according to many investigations, the ampullae in *Selachia* are, beyond a doubt, lateraliis innervated, any possible ampullar remainders, or formations homologous with the ampullae, will have to be looked for among the lateralis innervated organs. Considering that *Plotosus*, as previously stated, has canals with neuromasts, terminal buds and ampullae, while completely lacking free neuromasts and, consequently, pit-lines, a characteristic whereby, as far as present knowledge goes, this fish differs from all others, the pit-organs in *Plotosus* may, very reasonably, be supposed to have changed into ampullae. An additional reason for such a surmise is that the original position of the ampullae, i.e. where the ampullar canals open out in the epidermis, roughly corresponds to that of the pit-lines in the Silurids. Choosing the ampullar openings as starting-points, it should, thus, be possible to distinguish a nasal line, an accessory infraorbital line and, possibly, a posterior pit-line in the single upper ampullar group. In the ampullar group on the cheek, an oral line, an anterior pit-line and one or more opercular lines should prove discernible. But, as mentioned above, the actual innervation does not everywhere agree with the innervation of the postulated lines. These problems can only be settled by embryological investigations.

The canals.

It is to be regretted that the literature offers but very few data regarding the time and order of formation of the canals. From observations in the examined species it would appear, however, that they form in a specific order and that many characteristics, with regard to their formation, recur from one

species to another. In this respect, the Cyprinids constitute a uniform group, while *Nemachilus* essentially differs from the "Cyprinid type". With a view to securing some comparative material also from other fishes, I have studied the collection of sections from fishes at the Zootomical Institute of the University of Stockholm, for the particular purpose of ascertaining when, and in what order, the canals form. In this connection, my chief attention has been directed to the infraorbital, supraorbital and mandibulo-preopercular canals.

Clupea	29	mm	Preopercular canal.
„	32	„	All canals.
Coregonus lavaretus	21	„	Preopercular canal indicated.
Salmo salar	20	„	All canals, except the infraorbital, indicated.
„	27	„	All canals, except the infraorbital.
Galidichtys	15.3	„	Frontal[1] and mandibular canals.
„	17	„	Antorbital and preopercular canals.
„	22.5	„	Temporal canal.
„	32	„	Infraorbital canal.
Esox lucius	18.2	„	Frontal canal. Anterior part of preopercular canal indicated.
„	20.5	„	Nasal canal. Antorbital canal indicated.
„	32	„	Temporal canal.
„	40	„	Slightly developed infraorbital canal.
Lebistes	23	„	Mandibulo-preopercular canal.
Spinachia spinachia	28	„	Supraorbital, antorbital and preopercular canals.
Belone acus	25	„	Invagination of the anterior part of the preopercular canal indicated.
„	43	„	The anterior part of the mandibular and the entire preopercular canal.
„	62	„	The frontal canal, the antorbital part of the infraorbital canal, temporal and anterior body canals indicated.
Ammodytes tobianus	23	„	The frontal and the preopercular canals. The anterior part of the body canal.
„	35	„	All canals.
Gadus merlangus	15	„	All canals.
Perca fluviatilis	29	„	All canals.
Labrus spec.	10	„	Supraorbital, antorbital, mandibular and temporal canals.
Trachurus trachurus	17	„	All canals.
Bothus spec.	8.5	„	Antorbital, preopercular and body canals.

[1] The term frotal canal is here applied to the part of the supraorbital canal that lies in or on the frontal bone.

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Bothus spec.	12 mm	Mandibular and nasal canals.
„	14 „	Frontal canal.
„	28 „	No infraorbital canal.
Cottus bubalis	24.5 „	All canals.
Cyclopterus lumpus .	9 „	All canals.
Zoarces viviparus ...	21 „	Frontal canal.
„ ...	22 „	Preopercular canal.
„ ...	32 „	Infraorbital canal.
„ ...	40 „	Mandibular canal.

From the above data it is evident that the canals, not unexpectedly, form at very different times. In Acanthopterygii they seem, practically always, to form early, as compared to other fishes. Thus, in *Cyclopterus* all the canals form at a length of 9 mm, in *Bothus* most of the canals at 14 mm, in *Labrus* at 10, in *Trachurus* at 17, in *Cottus* at 24, in *Perca* at 29 mm etc. As far as the two last-mentioned fishes are concerned the canals, undoubtedly, form earlier. I have, however, not had any younger stages at my disposal. Further, the canals in these fishes are, in all instances, well developed with very wide lumina.

In addition, the canals form in a certain order. As a rule, the anterior part of the preopercular canal forms first. After that, or simultaneously, parts of the supraorbital canal and the mandibular canal appear. Every time the infraorbital canal develops last, and generally considerably late. Invariably, the antorbital part of the infraorbital canal forms first. In many fishes, there is no invagination of the middle and posterior parts of this canal. The anterior part of the main canal of the body mostly forms rather early.

Comparisons with the Cyprinids reveal that also in those fishes the canals form in the same order. As a rule, the anterior part of the preopercular canal develops first, then the anterior part of the frontal canal. In *Phoxinus*, however, the mandibular canal forms first, then the preopercular canal. As to the supraorbital canal, the frontal part appears first, then the nasal canal and the "canal antérieur". Throughout, the infraorbital canal develops last, mostly a considerable time after the others. Also in these fishes the antorbital part appears first, then the posterior part of the infraorbital canal and, far later, the part of the canal that lies in the first infraorbital bone. In some species no canals form in this region. A characteristic trait in the Cyprinids is, further, that the canals from the beginning do not form each in one coherent piece but, generally, in small portions round each neuromast. Thus, a row of canal elements, situated one after another, appears, fusing later. Sometimes, as usually in *Phoxinus*, this fusion does not take place and, consequently, a row of small independent canals will appear also in the adult. Most frequently, the canals in each canal bone will, however, fuse into one canal but, generally, no fusion of the canals takes place between the bones. Thus, in the mandibulo-preoper-

cular canal in *Leuciscus* (fig. 11), a canal appears in the dental-splenial bone, one in the angular-splenial and a long canal in the preoperculum. From this "Cyprinid type" *Nemachilus* differs in important respects. In that fish the infraorbital and temporal canals form far in advance of the other canals (fig. 36). At this stage, a coherent canal thus extends from the nasal point below the eye out on the body. Only at the 47 mm stage, which is 4—5 months older than the forementioned stage, the missing canals will form, an exceptional reversal in the order of formation of the canals, as far as all the above described fishes are concerned.

The formation of the respective canals in the Cyprinids, occurs very late, as compared to the above described fishes in general, but more particularly in comparison with the Acanthopterygii. As a rule, the canals do not begin to invaginate before the fishes have reached a length of c. 20 mm. This applies to *Leuciscus, Alburnus* and *Nemachilus.* In *Phoxinus* and *Tinca,* the invagination takes place only at a length of 40—50 mm. However, it takes a very long time till the canal system has reached its full development. In *Phoxinus,* the canal formation is finished only when the fish is sexually mature, in *Nemachilus* at a length of 47 mm, in *Alburnus* at 42 mm, etc. Thus, the canal formation in these fishes occupies a comparatively long period of time.

Certain fishes, such as *Cobitis taenia* and *Corydoras,* entirely lack canals. In those fishes no trace of any canals can be discovered, nor of the epithelial thickenings that, as a rule, precede the canal formation.

As far as the canal pattern on the head in the examined Cyprinids is concerned, there are some characteristic features common to all species. Thus, the posterior part of the preopercular canal is incomplete. It never reaches up to the temporal canal, as usually happens, e.g., in the Silurids. The canal may be more or less developed. It is particularly short in *Phoxinus* and *Nemachilus,* where, mostly, only the anterior, horizontal portion is to be found. In others, e.g., *Alburnus* and *Abramis* the canal is comparatively well developed but, nevertheless, it does not reach up to the temporal canal. As pointed out by Stensiö (1947), the preoperculum of the Teleosts consists only of the ventral part of the paleonisciform preoperculum, i.e. of bones that develop in connection with the ventral part of the preopercular line, while the bones that form in connection with the upper part of this line are much reduced and may appear in the shape of suprapreopercular bones. In the examined Cyprinids it is obvious that only the lower part of the canal has developed, while the upper part has gone more or less lost. The suprapreopercular bones are rare.

In this connection, the supraorbital canal attracts particular attention. As shown in the descriptions, this canal does not curve down behind the eye, to join the infraorbital canal, as usually in, e.g., the Silurids, but continues straight caudad towards the posterior edge of the frontal bone and out on the anterior part of the parietal bone. However, the canal never reaches to the supra-

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temporal commissure. As far as present knowledge goes, the Ostariophysi constitute the only group of fishes in which the canal exhibits such a course, even though more or less developed. As shown by NIELSEN (1942) and DEVILLERS (1944, 1947), the lengthened posterior part of the canal is homologous with the anterior pit-line. In such Silurids as *Clarias, Auchenaspis* and *Chaetostomus* (POLLARD 1892), the supraorbital canal continues a short distance caudad, after its fusion with the infraorbital canal. In all these fishes, this part of the canal lodges one neuromast, innervated by an intracranial branch of the n. ophthalmicus superficialis, either issuing from the nerve or leaving the ganglion separately (*Auchenaspis*). In the Silurids, this canal is occasionally directly continued by the anterior pit-line, e.g., *Ameiurus melas* (HERRICK 1901). In such a Characinid as *Erythrinus unitaeniatus* (SAGEMEHL 1885), also the supraorbital canal, after its fusion with the infraorbital canal, continues on the frontal bone and the anterior part of the parietal bone, where it curves laterad. The same observation has been made by ALLIS (1904) in other Characinids, though the canal, in many of these fishes, will bend laterad, already on the frontal bone, down towards the temporal canal. As previously mentioned, this has not been observed in any other recent fish families, while in the fossil, mainly paleozoic, Paleoniscids, identical observations have been made. In e.g., *Glaucolepis stensiöi* (NIELSEN 1942), the supraorbital canal passes through the nasal, frontal and parietal bones. NIELSEN states: "Through the frontal the canal runs chiefly in a posterior direction, except along a short stretch in the middle part of the bone, where it runs in a postero-lateral direction. From the frontal it continues in a posterior direction through the anterior part of the parietal, so that the pointed posterior end of the canal just reaches the radiation centre of the parietal." A comparison between NIELSEN's fig. 19 and e.g., *Abramis* (fig. 27) reveals striking similarities, as far as this canal is concerned. Also in this fish, as well as in *Leuciscus, Alburnus, Tinca* and *Phoxinus*, the canal assumes the same course, with a lateral curve in the middle of the frontal bone. From there the canal continues to the middle of the parietal bone. Both in *Glaucolepis* and *Abramis*, among others, the pores in the canal are turned laterad before the bend and mediad in the actual bend. Behind the bend all the pores in *Abramis* are lateral and the majority of the pores, at least those that lie on the parietal bone, in *Glaucolepis* likewise lateral.

In details, the innervation of this "canal antérieur" (fig. 41 A—F) varies a great deal from one species to another. The lateralis nerves do not, disclose the same course in any of the examined fishes. All the nerve branches of the lengthened canal are intracranial, issuing from the dorsal side of the trigeminofacial ganglion or from the n. ophthalmicus superficialis. The marked variations chiefly depend on whether the n. ophthalmicus superficialis V and VII leave the cranium through a common foramen or separately. In *Leuciscus, Phoxinus* and *Alburnus* the nerves pass together, while, in *Abramis, Tinca* and *Nema-*

chilus they are separate. The foremost of the intracranial branches, which, in *Alburnus*, issues from the extracranial part of the main nerve and, then, immediately passes through a small foramen, back into the cranium, innervates, in *Phoxinus* and *Alburnus*, one neuromast, in *Leuciscus* and *Nemachilus* two, in *Tinca* three and in *Abramis* four. To judge from the innervation, these organs correspond to the last organ in the supraorbital canal of the Silurids. The neuromasts situated behind these organs, 2—5 in number, are innervated by a nerve that, together with the n. oticus, issues from the dorsal side of the ganglion. These organs may, either, all lie on the frontal bone, as in *Phoxinus*, or, both on the frontal and the parietal bones, which is more usual, but, none the less, they must be regarded as homologous. As will be shown later, separate canal bones that are afterwards to fuse, secondarily, with either the frontal bone only, or with that and the parietal bone, will develop in connection with the forementioned organs.

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It may be of a certain interest to compare here the number of neuromasts in the various species. In spite of the close kinship of most of these species, and their classification to one and the same family, the number of neuromasts varies considerably from one species to another. The figures in the table below must be regarded as approximate, owing, partly, to the variability of the number of neuromasts in the different canals, from one specimen to another, partly to the difficulty of identifying the neuromasts that will form part of the canals in a fully developed canal system.

	Supra-orb.	Infra-orb.	Mandi-bular	Preoper-cular	Tempo-ral	Supra-temporal	Total
Leuciscus	10	15	6	10	3	6	50
Phoxinus	5	11	4	6	3	1	30
Alburnus	9	11	6	9	3	4	42
Abramis	15	18	6	14	3	5	61
Tinca	15	24	10	20	9	7	85
Nemachilus ..	6	11	2	5	3	1	28
Plotosus	5	7	5	3	2	0	22

From the above table it will be seen that the number of organs in the examined species of Cyprinids varies from 30 to 85. Without exception, *Tinca* lodges the greatest number of neuromasts in its canals. In comparison with the Cyprinids generally, *Nemachilus* shows a fairly small number of organs. *Plotosus* has only 22 organs.

The canal bones.

The significance of the canal bones and their ontogenesis has been the subject of many investigations. The views expressed by their authors have been contradictory.

VROLIK (1873) was, probably, one of the first to discuss the significance

of the canal bones. His examinations were performed on *Esox*. His conclusion was that the primary purpose of the bones was to protect the canals and the neuromasts lodged in them. WALTHER (1882), who, likewise, dealt with *Esox*, opposed this view, maintaining that the protection of the canals was a secondary function. WALTHER had discovered that the membranous part of the frontal bone formed first, and that it had obtained practically its full development before the canal component began to appear. Only secondarily the bone developed into a protection for the canal. This difference between dermal bones and canal protection, thus indicated by WALTHER, was more distinctly discernible in *Ameiurus* (MCMURRICH 1884, KINDRED 1919). In *Ameiurus*, the nasal bone, the infraorbital bones and the suprapreoperculum are formed as cylindrical bones round the canals. All of these bones remain unchanged also in the adult, except the nasal bone, where bone lamellae develop. The frontal bone forms, first, as a normal dermal bone. The separate canal bones that, secondarily, fuse with the lamellar bone appear only later. DE BEER (1937) has paid much attention to these conditions. I shall later return to his views. However, he does not seem to be absolutely convinced of the correctness of KINDRED'S account. He states: "The frontal is of considerable interest, if KINDRED'S description is correct." Also PEHRSON (1944 a) calls his data in question, stating that his examination does not definitely prove that the frontal bone forms as described above. From the description of the development of the canal bones in, for instance, *Phoxinus*, *Tinca* and *Nemachilus*, it is, however, perfectly clear that the lamellar and latero-sensory components may form separately from one another. This confirms the correctness of KINDRED'S views.

In more primitive fishes, the canal bones form in connection with the neuromasts. First, a tube-like bone appears round the canals. Only later it develops into a lamellar bone. In these fishes, the primary purpose of the canal bones seems to be to protect the canals. In more differentiated Teleosts, the two components form in different ways. The membranous component forms like an ordinary dermal bone, while the other component appears in connection with the canal system. In these fishes the canal bone has specialized in two different directions, viz. as a dermal bone and as a protective bone for the canal. That this contention is correct is evident from the conditions in such fishes as lack canals, e.g. *Cobitis taenia*. If there is no canals, no latero-sensory bone develops, which shows that its formation is dependent on the presence, or absence, of the canals. Its function is, in all likelihood, to protect the canals. On the other hand, in spite of the disappearance of the canal, the membranous part remains, in the shape of a dermal bone.

Another question that has often been discussed, in connection with the canal bones, is whether bones that develop round the same canal in different species are homologous. In 1884, SAGEMEHL expressed the opinion that certain bones are characterized by the fact that they contain canals. In the opinion of ALLIS

(1904), it is extremely likely that a certain bone, or part of a bone, that in a certain fish develops in connection with a certain part of the canal system, is without exception homologous with a bone, or part of a bone that forms in connection with the same part of the canal system in another fish. This view has been shared by the majority of writers who have paid attention to these questions, and has served as a basis of homologizations of considerable parts of the dermal bone cranium in the fishes. However, DE BEER (1937) propounded a different opinion. He bases his reasoning on the above-cited investigation by KINDRED. DE BEER suggests that, should the latero-sensory component form separately, there is nothing that prevents these bones from secondarily fusing with any bones whatever that happen to lie below the separate latero-sensory component. Consequently, it would not, a priori, prove possible to homologize bones in different fishes by means of the canals. This contention cannot be entirely rejected. In certain exceptional cases, the separate latero-sensory components may fuse with such dermal bones as should not, normally, lodge any canal elements, e.g., the canal bones, round the lengthened supra-orbital canal in the Cyprinids, that fuse with the parietal bone, or the supra-preopercular elements that fuse with the operculum. Everything seems to indicate that, on account of the different extension of the canal, special conditions apply in this instance. An examination of the canal bone, and the genesis of the underlying dermal bone, shows that these two bones have, in fact, nothing in common. Apart from these exceptional cases, however, the question whether DE BEER'S objections are justified or not remains. In my view, the conditions in the examined Cyprinids provide an answer also to this question. In principle, the identity of the membranous component may be said to be determined, at homologizations, by means of the latero-sensory component that forms part of it and, in particular, through the innervation of the organs contained in this latter component. Is it possible, then, to apply the same principle, when the latero-sensory component forms separately, and either fuses with the membranous component or remains free? As previously stated, regarding the development of the canal bones in, e.g., *Nemachilus*, the two components form, invariably, in connection with one and the same organ. Further, in more differentiated species, such as *Leuciscus*, in which the membranous components in the frontal bone forms as a dermal bone, also this bone develops in a certain relationship to the very organs from which, later, the latero-sensory bones appear. From this I regard it as proved that DE BEER'S objections are groundless, at least as far as the Ostariophysi are concerned, and that there is nothing to prevent a homologization of canal bones containing components that form separately.

An additional, much discussed question concerns the binary primordia of the canal bones. These primordia were first described by PEHRSON (1922) in *Amia* where he found this binary origin in all canal bones, except in the infraorbital

and rostral bone series. Later, this condition has been ascertained in several fishes. PEHRSON (1944 a) found it in the nasal bone in *Esox* and in the suprascapular bone in *Polypterus* (1947), but, owing to the rather advanced stage of the youngest specimen, the other bones could not be analysed. DEVILLERS (1944 a) found similar primordia in the frontal bone, the preoperculum and the pteroticum in *Salmo irideus*. On the other hand, in *Salmo salar* PEHRSON (1944 a) has not found any binary primordia, with the exception of the nasal bone. According to BAMFORD (1948), no canal bones develop from binary primordia in *Galeichtys felis*. In the fishes examined by me, a binary origin has been observed in several instances, though varying from one species to another. In *Phoxinus*, binary primordia are to be found in the splenial bones and the preoperculum, in *Tinca*, probably, at least in the preoperculum, and in *Nemachilus* only in the bones round the anterior part of the infraorbital canal. In this connection, it should be noted that this binary origin appears only in the primordia of the latero-sensory component, never on those of the lamellar part. In comparison with *Amia*, binary bone primordia are less usual in the examined Teleosts. Thus, there is no binary origin in the bones round the supraorbital canal, possibly with the exception of the nasal bone, where an indication of such an origin is often to be noticed. Binary primordia are particularly common in the bones belonging to the mandibulo-preopercular series.

The reasons of this binary origin have been the subject of thorough discussions by various authors, but, so far, no definite answer to the question has been supplied. PEHRSON, STENSIÖ, and others, attribute a phylogenetic significance to these binary primordia, presuming that old binary bone series reappear in them. HAMMARBERG, JARVIK, and others, reject this supposition, suggesting purely mechanical causes. Thus, HAMMARBERG (1937) considers that "das Herabsinken des Schleimkanals, das bei *Amia* stattfindet, Ursache einer Zweiteilung dessen, was eine morphologische Einheit ausmacht, sein könnte". Against this statement I should like to draw attention to the fact that the binary origin in the primordia, in the fishes analysed by me, appears before the canal begins to invaginate, and that the two primordia have often fused, before the invagination. Further, it has been suggested that the nerve to the neuromasts may pass through the blastema and the first bone primordia and thereby produce an impression of a binary origin. In certain instances, this is possible or probable, particularly in the nasal bones in the fishes examined by me, where the bone shows but an indication of such an origin in its caudal part. In all probability, the binary origin depends on the nerve. In other cases, the nerve has, no doubt, nothing to do with it. The proof lies in the fact that when, after a short time, the binary primordia have fused with one another into a single bone, the nerve does not pass through it but, as a rule, in front of it. Moreover, as mentioned above, no binary origin ever appears in the lamellar primordia, which should have happened, if the nerve actually caused a division of the

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primordium. The cause of the binary origin must, obviously, be looked for somewhere else. STENSIÖ (1947) states that the binary primordia "represent the bone elements of two primarily independent sensory line series" (see page 187, regarding the preoperculum in *Amia*). STENSIÖ, then, presupposes a double origin of the preopercular line in this fish, but according to investigations by HOLMGREN and PEHRSON (1949), there is no reason to suppose that this line should be double.

The appearance of the binary origin in the Cyprinids, on one hand, and in *Nemachilus,* on the other, is peculiar in one respect. In the former, the mandibulo-preopercular bone series develops from double primordia, while, in the latter, this binary origin is observed only in the anterior part of the infraorbital series. When these facts are placed in relation to the order in which the canals invaginate, the mandibulo-preopercular canal will be found to appear first, in *Phoxinus,* the infraorbital canal being the last of all. In *Nemachilus* the order is reversed. Thus, the bone primordia, in connection with the canals that are invaginated first, are found to be binary, while bone primordia connected with canals that are invaginated later are single. As previously shown, in Teleosts generally, the mandibulo-preopercular canal is the first to sink in, and, as a rule, the binary origin is discovered in the splenial bones and in the preoperculum. However, the fishes that have been examined, in this respect, are as yet too few to justify any definite conclusion as to whether any general relationship exists between the binary origin and the order of formation of the canals. The forementioned example seems, none the less, to indicate such an interrelationship.

The origin and derivation of the blastemas, from which the bones are, later, developed, are of special significance, in judging the nature of the canal bones. In 1891, KLAATSCH propounded a theory, based, partly, on observations in *Salmo,* that the osteoblasts immigrate from the epidermis, being thus of an ectodermal origin. After examinations chiefly of *Amia,* PEHRSON (1922, 1940), found a migration of osteoblasts from the epithelial cells that lie round the neuromasts. This immigration of ectodermal cells has been denied, and the theory strongly criticized, by several authors, most recently, after a renewed examination of the problem, by DEVILLERS (1947). His analyses of *Salmo* have failed to discover any connection between the epithelium and the osteoblasts. HARRISON (1895), as well as the forementioned author, emphasize that, when, at the preparation, the fish has been obliquely sectioned, resulting in a more or less tangential cut of the epithelium, pictures may be obtained that suggest a connection between the epithelium and the underlying mesenchymal tissue. In my opinion, this can only apply to the anterior nasal region. Further back on the head, perfect transversal sections will invariably be obtained, provided, of course, that the fish is carefully orientated before the sectioning. The characteristic breaking-down of the subcutaneous connective tissue below the

neuromasts has been interpreted, by HARRISON, SCHLEIP and DEVILLERS, as a result of the invagination of the canal, in the course of which this region is subject to a tension, which, in their view, fully explains the process. DEVILLERS (1947, page 78) adds: "Mais il serait bizarre que la migration se produise au moment ou l'os est déjà bien formé, alors qu'on ne peut la rencontrer plus tôt quand elle serait nécessaire." I have had opportunities to study numerous series of sections of *Salmo*, and my conclusion is that this fish is by no means suitable for studies of this problem. The same applies to *Leuciscus*. The most distinct pictures are obtained in fishes with a comparatively thick epidermis, such as *Phoxinus*, and, above all, *Tinca* and *Nemachilus*. As will be seen from the microphotographs, 61 and 62, a thick multi-stratal epithelium with numerous mucous cells is to be found in the last-mentioned fish. At the base of the epithelium lies a comparatively thick and well delimited layer of connective tissue threads, parallel to the surface, and below, a thick layer of thinly scattered connective tissue threads with a sparse amount of cells. This layer fills the whole space between the epithelium and the dermal bones. In this stratum of connective tissue, which, also comprises nerves, blood vessels and fat cells, the free canal bones (fig. 62) are situated. To judge from the histological picture, the formation of the latero-sensory component proceeds as follows: At a certain stage of the development, e.g., at a length of 33 mm in *Nemachilus*, the breaking-down of the subepithelial connective tissue, and the turning inwards of the free ends of the connective tissue threads, become distinctly discernible. It should be noted that this takes place before the canal begins to invaginate. Consequently, this breaking-down of the connective tissue can have nothing to do with the canal invagination. Between these split connective tissue threads a blastema appears, often slightly caudally to the neuromast. This blastema is particularly well delimited, whether binary or single. In it the canal bones will, afterwards form. DEVILLÆRS's above-quoted statement, viz. that the supposed migration would take place only after the formation of the bone is difficult to accept. However, the question of the provenance of the osteoblasts remains. KLAATSCH and PEHRSON have suggested that they originate from the epithelium. The blastema and the bone would, therefore, have an ectodermal origin. Against this theory of PEHRSON, DE BEER (1937), among others, has raised the objection that, accordingly, it would not be possible to homologize, e.g., a frontal bone in a fish with similarly termed bones in higher vertebrates, owing to the ectodermal and mesodermal origin, respectively, of these bones. The provenance of certain cells is always very difficult to determine from histological picture only. Already earlier, PEHRSON has pointed out that the blastemas and first bone primordia do not lie straight below the neuromasts, but slightly caudally to them. In the fishes examined by me, I have made the same observations. A close study of these conditions will show that the blastemas constitute a more or less direct continuation of the placodes that were

left between the neuromasts, in the shape of a connecting strand, after their differentiation. As pointed out in the fore-cited page, the original placode does not disappear completely, but is found also in older fishes. As shown in experiments by DEVILLERS, it is probable that the neuromasts exert an inductive effect on the bone formation. At a certain stage of development, the neuromasts should induce the remainder of the placode in their close proximity into blastema and bone formation. This would, in addition, explain why no bones form in connection with the pit-line organs. As previously pointed out, only the primary neuromasts, i.e. those that will, later, for the most part be found in canals, develop from placodes, while the others originate otherwise. For my own part, I consider this interpretation to be purely hypothetical. Experimental investigations are indispensable to determine definitely the genesis of the osteoblasts, DEVILLERS has initiated such investigations, without, in 1947, having been able to report any results. It is to be hoped that he will be successful in his endeavours to furnish a definite answer to this important question.

As described earlier, the latero-sensory and lamellar parts of the canal bones may either be united from the beginning or secondarily fuse with one another or remain entirely separate. The third possibility has been known for a long time but, on the whole, barely mentioned. Thus, SAGEMEHL (1885, 1891) found that the canal bones, in *Gymnotus* and certain Murenids and Cyprinids, lay enclosed in separate bone cylinders. In SAGEMEHL's opinion, the explanation was that the epidermis in these fishes was thick and that the underlying dermal bones, for this reason, were deeply sunk in the skin. If the canals, and the organs lodged in them, were to perform their function, according to SAGEMEHL, they must not sink too deep in the epidermis. On this account the canal cylinders occupy a more superficial position. ALLIS (1935) supposed that the canal bones in *Polyodon* and *Acipenser* are made up of two canal components. He speaks of "a latero-sensory component" and "a membranous component", a terminology that has been adopted also in the present paper. PEHRSON (1947) has found free splenial bones in *Polypterus*. In a previous chapter in this work it has been pointed out that free cylindrical bones are to be found in *Nemachilus* and, to a certain extent, also in *Tinca*. As compared to other examined species, the forementioned fishes posses a particularly thick epidermis. In *Tinca*, it may be added, it is possible to ascertain that, in the canal bones that lie close to the epithelium, the two components fuse, while bones that lie deeper down remain separate. This supports SAGEMEHL's theory that the thickness of the epidermis is a determining factor in this respect. A similar condition might be expected also in other fishes, particularly in those with a thick epidermis, e.g. in *Anguilla*, but in that fish the two components are, on the contrary, found to be closely united. However, an examination will show that the canals invaginate at the elver-stage, when the epidermis is, as yet, comparatively thin.

Only after the metamorphosis it begins to thicken. At that time, however, the canal, and the bones allied to it, have already formed. Thus the conditions in this fish are specific, and the interpretation given above remains unaffected.

VII. SUMMARY.

As stated above, the examined species have many traits in common. They may be specified as follows:

1. The pit-line system is particularly well developed.
2. The line system of different species has, to begin with, a uniform appearance.
3. The first appearing neuromasts, the primary ones, will in the course of their further development, chiefly become canal neuromasts.
4. The primary neuromasts that are not enclosed in canals are homologous with the canal neuromasts in lower forms of Actinopterygii. These "primary pit-lines" are the rostral commissure, the antorbital line, the nasal line and the anterior mandibular line.
5. From the primary sense organs secondary organs may be detached, forming secondary pit-lines. They are the lateral supraorbital line, the accessory infraorbital and the accessory preopercular line, the opercular lines and the medial extrascapular line. Also the free oticus- and glossopharyngeus-innervated organs, may belong to these secondary pit-lines.
6. All the canals are accompanied by lines, parallel to them, formed as stated in the above paragraph. Thus, the supraorbital canal is accompanied by a lateral line, the infraorbital and preopercular canals by accessory lines, the temporal canal by a number of free organs and the supratemporal commissure by the extrascapular line.
7. A third group of pit-lines comprises those that form in other ways than those described in paragraphs 5 or 6, viz. the horizontal and the vertical line on the cheek, the medial supraorbital line and the symphysial line.
8. In the examined Cyprinids, the horizontal and the vertical line have an orientation that differs from the common pattern, in so far as the horizontal line, from an embryological point of view, is the vertical line, and vice versa. This changed orientation is explained by the pronounced changes that take place on the ventral and ventro-lateral sides of the head, on account of the strong development of the nose portion and of the forward growth of the mandible.
9. The canal system is comparatively feebly developed, and suffers certain constant reductions.
10. The canal system begins to develop and becomes fully developed rather late, in some cases only when the fish is sexually mature.

11. Certain canals form in a way that differs slightly from that common in Teleosts. This applies particularly to the earliest invaginated canals, viz. the mandibulo-preopercular canal.
12. The canals first form round each neuromast. The separate canals later fuse, to a varying extent, with one another.
13. In the Cyprinids, the anterior part of the preopercular canal as a rule forms first, then the mandibular or the frontal canal. After this, the nasal, canal, the "canal antérieur" and the temporal canal appear. Invariably, the infraorbital canal forms last. Of this latter canal, the antorbital part always comes first, then the posterior part within the region of the second and third infraorbital bones, and far later, the part situated in the first infraorbital bone. Within this latter region, canals may fail to appear.
14. In *Nemachilus* the canal formation takes place in a reversed order. Here, the infraorbital canal comes first, simultaneously with the temporal canal. Far later, the other canals appear.
15. In all the species, the upper part of the preopercular canal is lacking. Thus, the canal never reaches up to the temporal canal.
16. Behind the eye, the supraorbital and infraorbital canals do not meet.
17. The supraorbital canal continues out towards the posterior edge of the frontal bone and, in certain species still further, viz. to the middle of the parietal bone. The posterior part of the supraorbital canal is homologous with the anterior pit-line. Considerable similarities in the course of this canal, between Cyprinids and Paleoniscids, have been pointed out.
18. The ampullae of Lorenzini in the Silurid *Plotosus anguillaris* are, probably, homologous with free neuromasts.
19. The fully developed canal bones in the examined Cyprinids have, roughly, the same appearance and form.
20. On the other hand, the bones form and develop in slightly different ways in the different species. This, above all, applies to the interrelationship of the latero-sensory and the lamellar component. In *Leuciscus,* the two components are mostly, from the beginning, united with one another. In *Alburnus, Phoxinus* and *Tinca,* the two components form separately, fusing with one another, in the course of the development. In *Nemachilus,* all the cylindrical bones round the canals remain separate, except those in the antorbital bone.
21. In *Cobitis taenia,* which lacks canals, also the latero-sensory component is, invariably, absent. However, the membranous part of the canal bones is left.
22. In the Cyprinids, the bones that form in connection with the mandibulo-preopercular canal develop, without exception, from binary primordia, the others from single primordia.
23. In *N. barbatula,* on the other hand, only the bones that form round the

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anterior part of the infraorbital canal develop from binary, all the other bones from single primordia.

24. Only the latero-sensory component has a binary origin. The lamellar part of the bones always develops from single primordia.

25. When these facts are considered, in relation to the time of formation of the various canals, the bones that form in connection with the first invaginated canals are found to be binary, while the bones appearing in connection with those invaginated later become single.

26. The latero-sensory component is separate in fishes with a thick epidermis, but fuse with the underlying bone in fishes with a thinner epidermis.

27. The blastemas of the latero-sensory bones probably originate from such remainders of placodes as are left between the primary neuromasts, the so-called "connecting strand". This would explain why no bones develop in connection with pit-lines.

28. The nasal bone forms as two or several separate bones that later fuse into one bone. In *N. barbatula*, the bones remain separate. *C. taenia* lacks this bone. The lamellar part is missing in all the examined species.

29. In *Leuciscus* and *Phoxinus* the lamellar part of the frontal bone forms in the shape of a number of small bone strips in the subcutaneous connective tissue, without any previous blastemas, and without any notable relationship to the neuromasts. In *N. barbatula*, first a blastema appear, then the bone develops in the proximity of the neuromasts. The latero-sensory part of the bone forms far later.

30. In connection with the "canal antérieur" a number of canal bones form, that will fuse either with the underlying frontal bone or with that bone and the parietal bone.

31. The lamellar part of the antorbital bone develops comparatively early from a blastema that forms in connection with the anterior part of the infraorbital line. Considerably later also the latero-sensory component will arise from the same neuromasts.

32. In the Cyprinids, the infraorbital bones invariably form very late. The foremost infraorbital bone appears last. In *N. barbatula*, on the other hand, these bones arrive early and in a comparatively large number. In this fish the number varies from one specimen to another. *C. taenia* lacks infraorbital bones.

33. In the Cyprinids, the pteroticum is a complex bone, formed by a latero-sensory component, consisting of two intertemporal bones, one supratemporal and one membrano-pterotic bone, developed in the same way as the lamellar part of the frontal bone in, e.g., *Leuciscus*, and, in addition, a cartilage-bone, the opisthoticum. In *N. barbatula*, the membranous component is missing. In *C. taenia*, both the membranous and the latero-sensory component are absent.

43. In *Phoxinus, Tinca* and *Nemachilus,* the splenial bones form separately. In the first-mentioned species they fuse with the dental bone. In the others they remain separate. *N. barbatula,* however, lacks the dental-splenial bones.

35. The preoperculum forms in a blastema that appears below the preopercular neuromasts. Far later, immediately before the invagination of the canal, the latero-sensory component forms in connection with the same neuromasts, one bone corresponding to each neuromast.

36. The suprapreoperculum has been found only in *Alburnus,* where it has fused with the operculum.

VIII. ABBREVIATIONS.

a.io.l. accessory infraorbital line of pits
a.m.l. anterior mandibular line of pits
a.n.a. anterior nasal aperture
ang. angular bone
ang.c. part of the mandibular canal lying in the angular bone
ang-sp. angular-splenial bone
ao. antorbital bone
ao.bl. blastema of antorbital bone
ao.c. part of the infraorbital canal lying in the antorbital bone
ao.l. antorbital line of pits
ao.l-s. latero-sensory part of the antorbital bone
a.po.l. accessory preopercular line of pits
asph. autosphenoticum
a.v. auditory vesicle
b.ml.c. bones round the main lateral canal of the body
c.a. "canal antérieur"
c.a.o. organ(s) in the "canal antérieur"
c.am. canal of ampullae
cm. corono-meckelian bone
d.am. dorsal field of ampullae
d.art. derm-articular bone
dc. dental bone
dc-sp. dental-splenial bone
e.b. epiphysial bridge
ecm. ectethmoid bone
ecpt. endopterygoid bone
ep. epithelium
ept. ectopterygoid bone
es.l. lateral extrascapular bone
es.m. medial extrascapular bone
f V foramen for the nervus trigeminus
f VII foramen for the nervus facialis
f IX foramen for the nervus glossopharyngeus
f X foramen for the nervus vagus
f.o. foramen for the nervus oticus
fo.hy. fossa for the hyomandibular bone
fr. frontal bone
fr.bl. blastema of frontal bone
fr.c. part of the supraorbital canal lying in the frontal bone
fr.l-s. latero-sensory part of the frontal bone
gc. gill-cover
h.l. horizontal line of pits
hy. hyomandibular bone
io. infraorbital bone
io.c. infraorbital canal
io.l. infraorbital line of pits
io.p. infraorbital placode
it. intertemporal bone
it.c. part of the temporal canal lying in the intertemporal bone
it.o. intertemporal organ(s)
it-st. intertemporo-supratemporal bone
l.am. lateral field of ampullae
l.o.l. lower opercular line of pits
l.so.l. lateral supraorbital line of pits
l-s.e.pa. latero-sensory element in the parietal bone.
max. maxillary bone
m.c. mandibular canal
me.ca. Meckel's cartilage
mes. mesethmoid bone

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m.cs.l. medial extrascapular line of pits
mes.pr. primordium of the mesethmoid bone
m.j. mandibular joint
m.l. mandibular line of pits
m.l.c. main lateral canal of the body
m.l.o. sense organ(s) in the main lateral line of the body
m.l.p. placode of the main lateral line of the body
mm. mento-mandibular bone
m.p. placode of the mandibular line of pits.
m.so.l. medial supraorbital line of pits
m-pt. membrano-pterotical bone
na. nasal bone
na.c. part of the supraorbital canal lying in the nasal bone
na.l. nasal line of pits
na.p. placode of the nasal line of pits
na.pr. primordia of the nasal bone
na.s. nasal sac
nch. notochord
n.bucc. nervus buccalis
n.gph. nervus glossopharyngeus
n.h.l. nerve to the horizontal line of pits
n.hy. nervus hyoideus
nm. neuromast
n.m.e. nervus mandibularis externus
n.m.i. nervus mandibularis internus
n.o. nervus oticus
n.opht. nervus ophthalmicus superficialis
n.o.s. nervus opercularis superficialis
n.v. nervus vagus
n.v.l. nerve to the vertical line of pits
o. operculum
oc.l. occipitale laterale
o.o. opercular sense organ(s)
oot. opisthotic bone
o.p. placode of the oticus-innervated sense organs
or.l. oral line of pits
pa. parietal bone
pal. palatine bone
pmax. premaxillary bone
p.n.a. posterior nasal aperture
po. preopercular bone
po.bl. blastema of the preopercular bone
po.c. preopercular canal
po.l. preopercular line of pits
po.l-s. latero-sensory part of the preopercular bone
po.p. placode of the preopercular line of pits
poot. prootical bone
pr.ph. processus pharyngeus
pr.ra. processus retroarticularis
ps. parasphenoid bone
q. quadrate
q-j. quadato-jugal bone
ra. retro-articular bone
r.c.p. rostral commissure of pits
ros. rostral bone
sbop. subopercular bone
scl. supracleitral bone
shy. stylohyal bone
so. supraorbital bone
so.c. supraorbital canal
so.l. supraorbital line of pits
so.p. placode of the supraorbital line of pits
spir. spiraculum
spo. suprapreopercular bone
spo.l. suprapreopercular line of pits
st. supratemporal bone
st.c. part of the temporal canal lying in the supratemporal bone
st.com. supratemporal commissure
st.com.o. sense organ(s) in the supratemporal commissure of pits
st.o. supratemporal sense organ
sym. symphysis
sym.l. symphysial line of pits
symp. symplectic bone
t.c. temporal canal
t.m.a. taenia marginalis anterior
t.m.p. taenia marginalis posterior
t.o. temporal sense organ(s)
tr.hy. truncus hyoideo-mandibularis
t.syn. tectum synoticum
u.o.l. upper opercular line of pits
v.l. vertical line of pits
v.o.l. vertical opercular line of pits

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THE EMBRYONIC DEVELOPMENT OF THE HAND AND FOOT OF EREMITALPA (CHRYSOCHLORIS) GRANTI (BROOM)

BY

MÄRTHA KINDAHL

(With 19 figures.)

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For this investigation of the embryonic development of the hand and foot of Eremitalpa (Chrysochloris) Granti (BROOM), five embryos with a body length of respectively 9 mm, 10 mm, 12 mm, 19 mm, and 25 mm, and some full-grown specimens have been at my disposal. These embryos were obtained by Professor N. HOLMGREN from Professor C.-J. VAN DER HORST, Johannesburg, South-Africa.

THE HAND.

In the embryo at the earliest stage of development that has been at my disposal, with a body length of 9 mm, the third finger is most developed (fig. 1). It consists of rudiments of a carpal (fig. 2, ca_3), a metacarpal (m_3), and three phalanges (*1—3*). The metacarpal is most developed and consists of procartilage as the other rudiments, except the third phalange, which is a mesenchymatic concentration.

Also in the second finger, the metacarpal (m_2) is most developed and consists of procartilage, but it is considerably smaller than that of the third

Fig. 1. Eremitalpa Granti. Hand of embryo 9 mm.

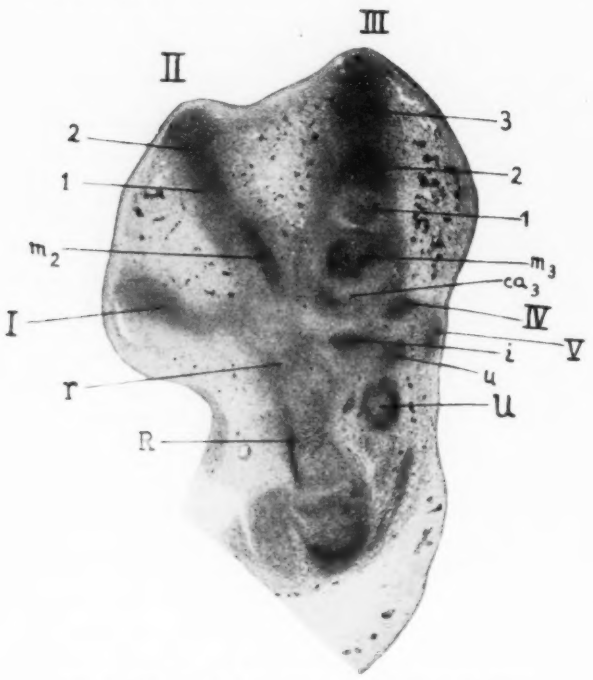

Fig. 2. Embryo 9 mm, horizontal section of hand.

finger (m_3). Proximally to the rudiment of the metacarpal, there is the rudiment of carpal 2 (fig. 3, ca_2) consisting of a concentration of the mesenchyme. For the rest, the second finger is represented by a string of mesenchyme with two concentrations of cells, which are the rudiments of phalange cartilages.

In the string of mesenchyme that represents the first finger (I), there is only a very small procartilage, which is probably the carpal (ca_1). Two faintly discernible concentrations of cells represent the rudiments of metacarpal I (m_1) and the first phalange.

The mesenchymatic string of the fourth finger is considerably shorter than those of the other fingers. Two concentrations of cells with a beginning condrification can be discerned here. They represent carpal 4 (ca_4) and the rest of the finger.

A faint indication of the rudiment of a fifth finger (V) is found as a concentration of cells close to the fourth finger. Another concentration of cells, which also probably belongs to the rudiment of the fifth finger, lies immediately below the skin. It continues in a tendon. The protuberance of the fifth finger is extremely small. The skeleton parts of the first four fingers, however, correspond to well developed protuberances (fig. 1).

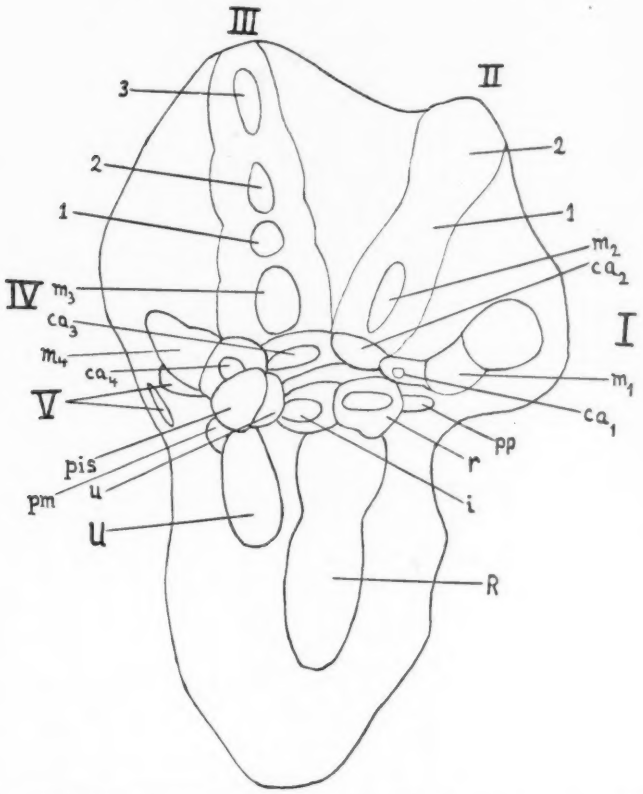

Fig. 3. Embryo 9 mm, diagrammatical reconstruction of hand from the palmar side.

A small rudiment of a praepollex (fig. 3, *pp*) appears as a string of blastema laterally to the rudiment of the radial, somewhat distally to the rudiment of the carpal of the first finger.

In the central part of the carpus there is found the intermedium (*i*), and distally to the radius the radial (*r*) has developed. Both consist of procartilage. In the distal continuation of the ulna two procartilages are found. Of these, one represents the ulnar (*u*) and the other, which is somewhat laterally situated, perhaps the postminimus (*pm*). Towards the palm of the hand the rudiment of the pisiforme is situated (*pis*).

In an embryo, 10 mm long, it was already possible to state that very important changes have taken place. In the third finger, which also at this stage is the most developed one, the rudiments of all the three phalanges consist of procartilage. The rudiment of the first phalange consists of a very small cartilage (fig. 4, *1*), which lies not only very close to phalange 2 (*2*) but equally near the cartilage rudiment of the large metacarpal (m_3). This cartilage

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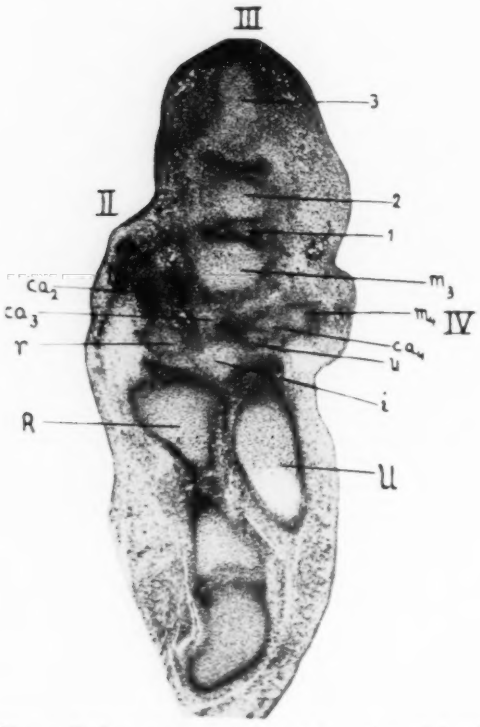

Fig. 4. Embryo 10 mm, horizontal section of hand.

rudiment sends out a semicircular lamella towards the second phalange. This lamella tends to enclose the first phalange. In this way phalange 1 lies wedged between phalange 2 and the metacarpal. A reduction of the number of skeleton elements in the third finger thus has begun. The rudiment of carpal 3 (ca_3) consists of a fairly large cartilage.

The second finger, which is considerably narrower than the third, possesses three distinct phalange rudiments (fig. 5). All, except phalange 3 which is only a concentration of mesenchyme, consist of procartilage. The metacarpal (m_2) is a large procartilage and more developed than the rudiments of the phalange cartilages. The carpal (ca_2) is represented by a cartilage rudiment immediately proximally to the metacarpal. It is not so large as the corresponding element of the third finger. There is no indication of a fusion between the rudiments of the various skeleton parts of the second finger as in the third.

The skeleton rudiments of the fourth finger seem to be three (fig. 5, *IV*). In all of them the formation of cartilage has begun, though in varying degrees. Metacarpal IV (fig. 4, m_4) is the most developed but carpal 4 (ca_4) is also well developed. Two rudiments of phalanges are seen (fig. 5, *IV*, *1* and *2*).

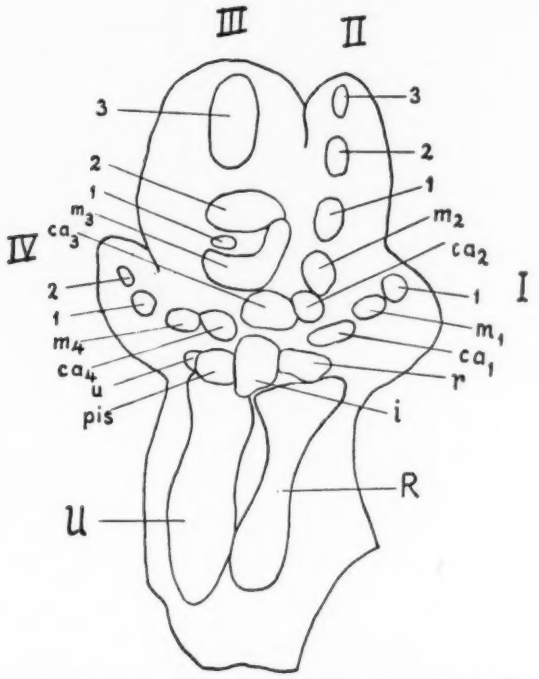

Fig. 5. Embryo 10 mm, diagrammatical reconstruction of hand from the palmar side.

In the first finger both a carpal and a metacarpal have developed, but there is only one phalange cartilage rudiment present (fig. 5, *1*).

Thus at the 10 mm stage four carpals and four metacarpals are developed. In the most developed third finger as well as in the second the number of phalange cartilage rudiments is three. The fourth finger has only two and the first finger only one phalange cartilage rudiment.

The radius and the ulna have grown. Their central parts consist of cartilage, and the remaining parts of procartilage, except the epiphyses which for the greater part still consist of concentrations of the mesenchyme. Distally to the radius and the ulna two procartilages occur, probably representing the radial and the ulnar. Of these the radial is the larger. Between the radial and the ulnar there is the very large cartilage rudiment of the intermedium. Towards the palm of the hand distally to the ulna lies the pisiforme (fig. 5, *pis*).

At the 12 mm stage (fig. 6) the commencing reduction of the number of cartilages of the third finger is clearly discernible. The metacarpal (m_3) is now much larger. Also the second phalange has grown considerably. These two cartilages lie very near one another, only a narrow interspace between them and the very little phalange 1 is discernible. From the basal part of the

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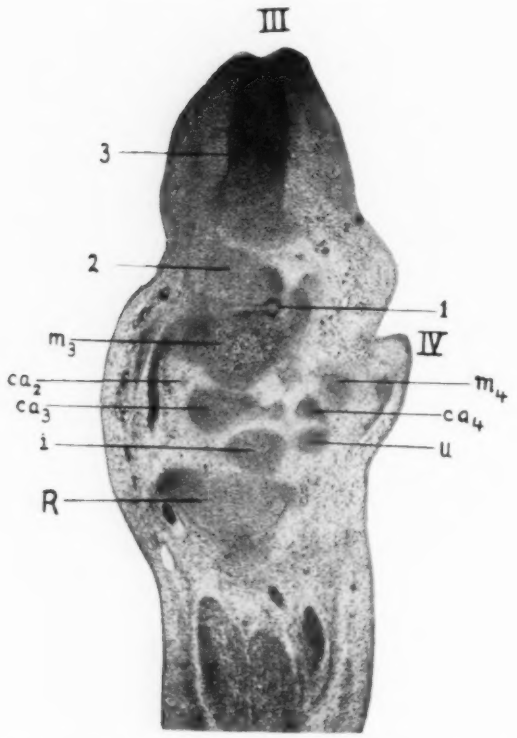

Fig. 6. Embryo 12 mm, horizontal section of hand.

metacarpal there extend protuberances to the sides, owing to which the cartilage has become much broader. The cartilage of the third phalange (*3*) has grown considerably, and also its basal part has become broader owing to lateral protuberances. Carpal 3 (ca_3) is supplied with a small protuberance towards the side of the ulna (figs. 6 and 7) and has thus become broader.

The rudiments of the phalange cartilages of the second finger have developed considerably from the preceding stage (fig. 7). They have all grown, and the third phalange cartilage rudiment now consists of procartilage like the rest. The metacarpal II (m_2), which is the largest cartilage of the finger, is somewhat broader in its end parts. Carpal 2 (fig. 8, ca_2) is connected with metacarpal II (m_2) by means of a string of cells.

The first finger is least developed, possessing only two rudiments of phalange cartilages (fig. 7). Metacarpal I (m_1) is somewhat broader than the phalange cartilages. Carpal 1 (ca_1), which is smaller than the carpals of the other fingers, is connected with metacarpal II by means of a string of cells (figs. 9 and 10). At one place it also touches metacarpal I (fig. 7).

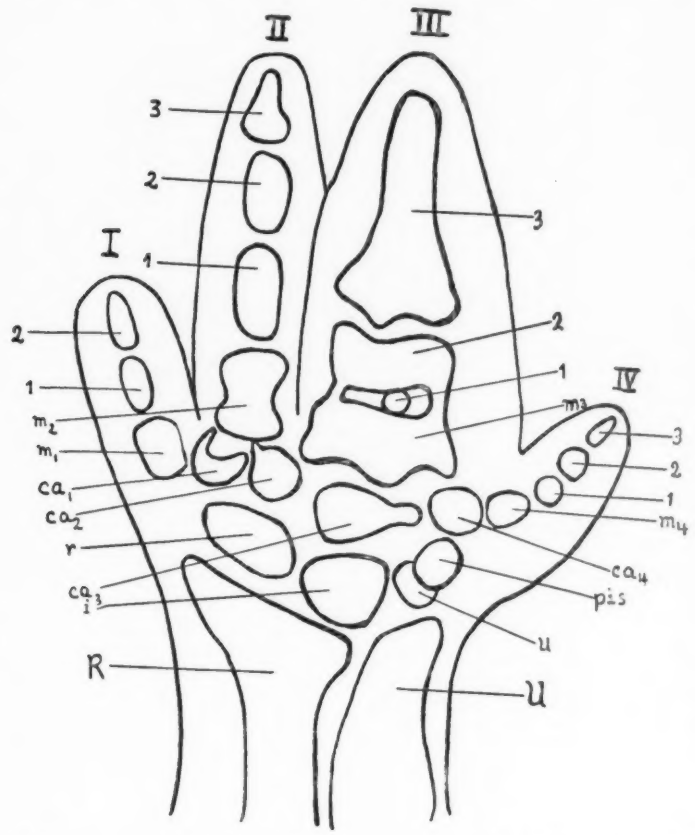

Fig. 7. Embryo 12 mm, diagrammatical reconstruction of hand from the palmar side.

Thus at this stage metacarpal II is connected both with carpal 1 and carpal 2 (fig. 7).

The fourth finger has the rudiments of three phalange cartilages, the third of which is somewhat smaller and less developed than the others. Metacarpal IV as well as carpal 4 are well developed (fig. 7).

The proximal row of carpal cartilages, the radial, the intermedium and the ulnar, have also grown, as well as the pisiforme.

No rudiments of any centrals have been observed.

In an embryo 19 mm long the development of the skeleton elements of the hand has advanced considerably. All cartilages have come into contact with each other and formed articulations (fig. 11). Ossification has begun in the radius and the ulna and also in the distal end part of the third phalange cartilages.

The last phalange cartilage of the third finger has grown enormously in length, and its basal part, which articulates with the compound cartilage

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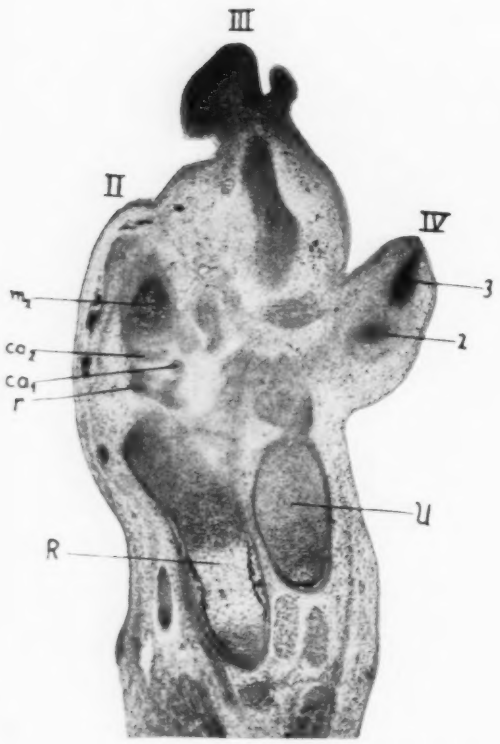

Fig. 8. Embryo 12 mm, horizontal section of hand.

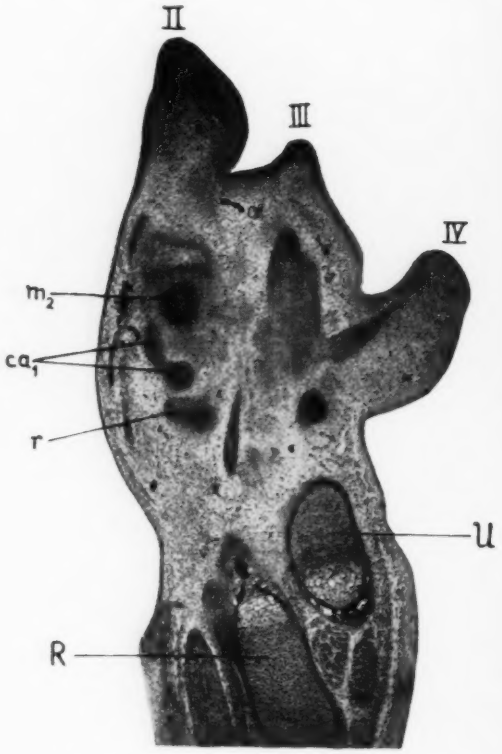

Fig. 9. Embryo 12 mm, horizontal section of hand.

($1+2+m_3$), also considerably in width. The third phalange is quite covered by a nail. The various components of the compound cartilage, which were distinctly visible at the two preceding stages, have now completely fused. Only a canal, through which a blood-vessel runs, indicates where the fusion took place. At one edge of the canal the small first phalange cartilage seems to have got attached (fig. 11, *1*). The compound cartilage articulates proximally with carpal 3 as well as with carpal 4.

The number of cartilages of both the second and the fourth finger has been reduced. Fusion has taken place between the first and second phalange cartilages. The canal of a small blood-vessel indicates where the fusion took place. In horizontal sections through the cartilages in question two centres are seen, one on each side of the blood-vessel (figs. 12 and 13, *1* and *2*).

In full-grown animals (figs. 14 and 15) the skeleton parts of the hand are fewer in number than in the embryos. The embryonic stages have shown how the reduction has taken place. The most developed third finger only consists

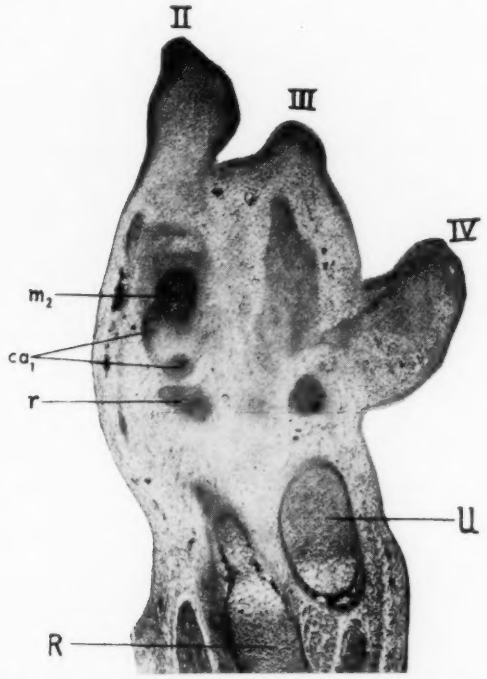

Fig. 10. Embryo 12 mm, horizontal section of hand.

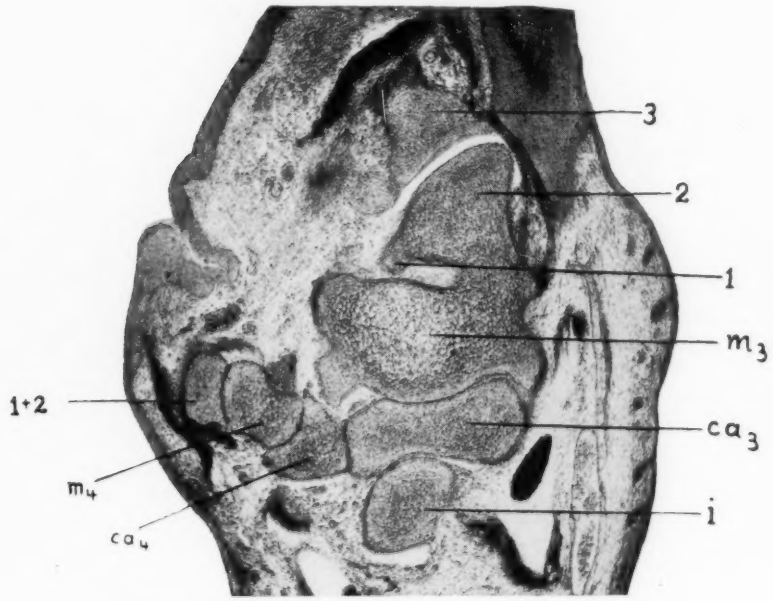

Fig. 11. Embryo 19 mm, horizontal section of hand.

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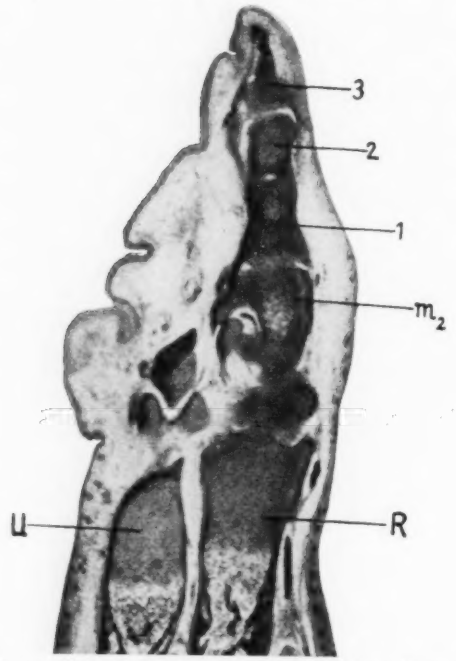

Fig. 12. Embryo 19 mm, horizontal section of hand.

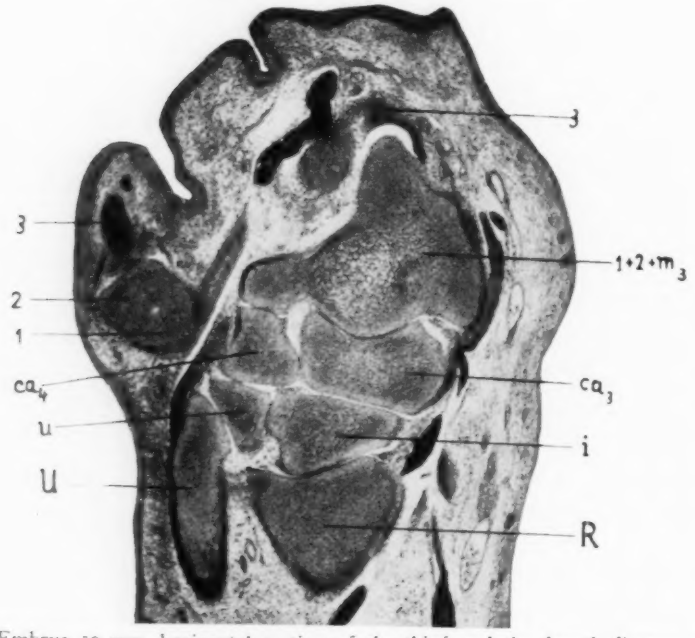

Fig. 13. Embryo 19 mm, horizontal section of the third and the fourth fingers of hand.

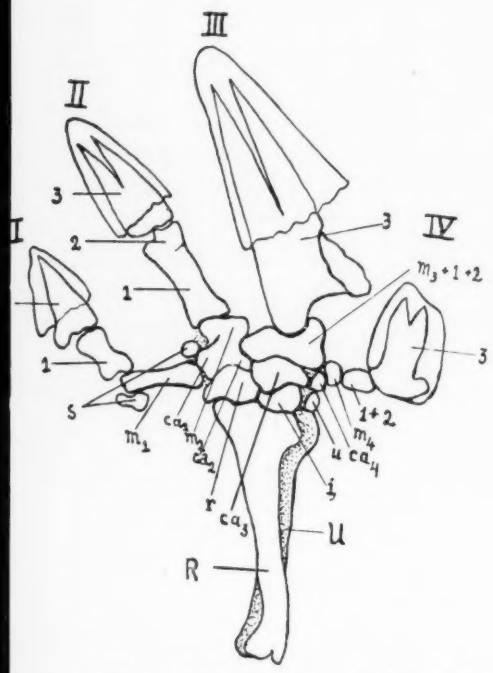

Fig. 14. Adult, hand from the dorsal side.

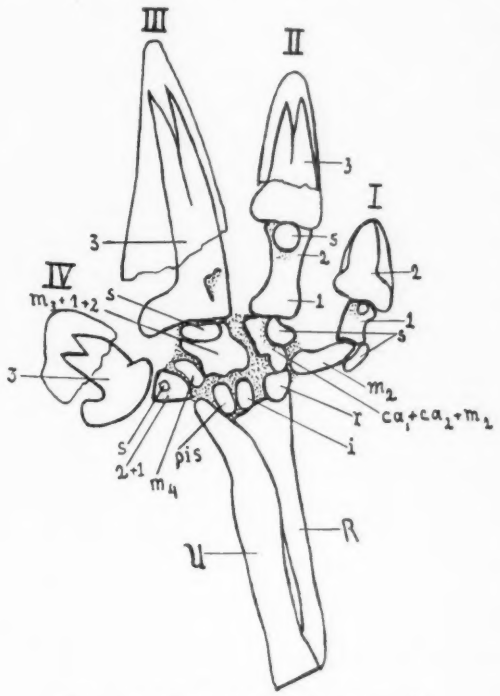

Fig. 15. Adult, hand from the palmar side.

of one phalange—the last. The first and the second have fused with metacarpal III.

In the second finger there are two bones. The proximal is composed of the first two phalanges, a faint dividing line indicating the place of fusion, and the distal is the third phalange.

The first finger consists of three bones, namely the metacarpal I and two phalanges. It is noteworthy that the metacarpal looks like a finger phalange.

The fourth finger, which is the smallest, has at the embryonic stages three phalange cartilages, of which the first and second fuse and together form one of the two phalanges of the finger. The metacarpal bone of the fourth finger is a free element.

The metacarpal part of the hand has become much shorter though phalange elements also take part in its formation. Metacarpal I, as has already been mentioned, forms part of the finger itself. On the other hand, metacarpal II has been united with carpal 2 as well as carpal 1. The first sign of this fusion appeared at the 12 mm stage (figs. 7—10). Metacarpal III has been united with the first and second phalanges. This fusion began already at the 10 mm stage (fig. 4). Metacarpal IV is independent.

Only two carpals appear as independent bones, namely carpal 3 and carpal 4. Carpals 1 and 2 have, as has been mentioned above, fused with metacarpal II. The proximal row of the bones of the carpus consists of the radial, the intermedium, the ulnar as well as the pisiforme.

At the finger articulations, sesamoids occur (figs. 14 and 15, *s*).

Parallel with the radius and the ulna, the wellknown bone is situated which is the ossified tendon flexor digitorum communis profundus.

THE FOOT.

At the 10 mm stage the foot is shaped like a spade and is supplied with five small protuberances which represent the toes (fig. 16). Of these the second, the third and the fourth are somewhat larger than the first and the fifth. All the toes are supplied with a metatarsal (*m*) which is, however, most developed in the first-mentioned three toes. Here also a first phalange cartilage appears in the concentrated mesenchymatic strings which radiate from the central part of the foot towards the protuberances in the periphery. Immediately proximally to the rudiments of the metatarsals five tarsals are seen, the fourth of which is the largest (ta_4). It is connected with the fifth tarsal (ta_5) by means of a cell bridge.

In the centre of the tarsus there appear rudiments of many skeleton parts. Distally to the tibia (*T*) as well as to the fibula (*F*) a concentration of mesenchyme is seen, being the rudiments of the tibial (*t*) and the fibular (*f*). Between them there is a large cartilage rudiment, which probably represents the central 1 (c_1). Immediately proximally to it a mesenchymatic concentration is seen, which is probably the rudiment of the intermedium (*i*). Opposite tarsals 2 and 3 there is a fairly large cartilage rudiment. To judge from its position, it does not seem improbable that it is formed from the centrals 2 and 3 (c_2+c_3). A distinct limit between the two components is, however, difficult to discern. Between the rudiments of the fibular (*f*) and tarsal 4 (ta_4) there is a large cartilage rudiment, no doubt the central 4 (c_4).

In an embryo 12 mm long, the toes are well developed, and the skeleton parts of the foot have advanced considerably (fig. 17). In the larger cartilage rudiments such as the tibia and the fibula as well as the metatarsals the procartilage tissue has begun to be chondrified. In the three most developed toes, the second, the third and the fourth, three cartilage rudiments of phalanges are seen, the third of which essentially differs, on account of its lengthened conical form, from the first and the second which are round. Also in the fifth toe three cartilage rudiments of phalanges are seen, the third, however, appearing extremely faintly. In the first toe there are only two rudiments of phalanges, the second of which consists of mesenchyme.

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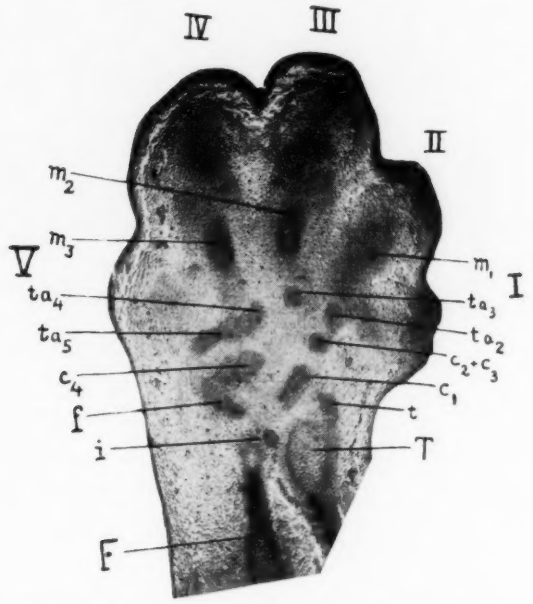

Fig. 16. Embryo 10 mm, horizontal section of foot.

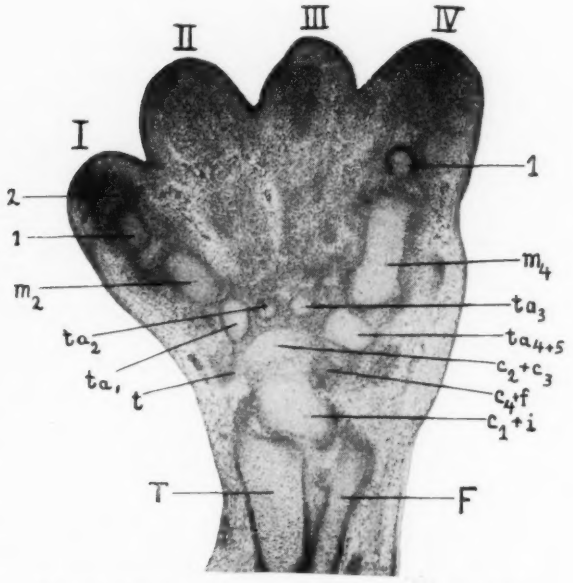

Fig. 17. Embryo 12 mm, horizontal section of foot.

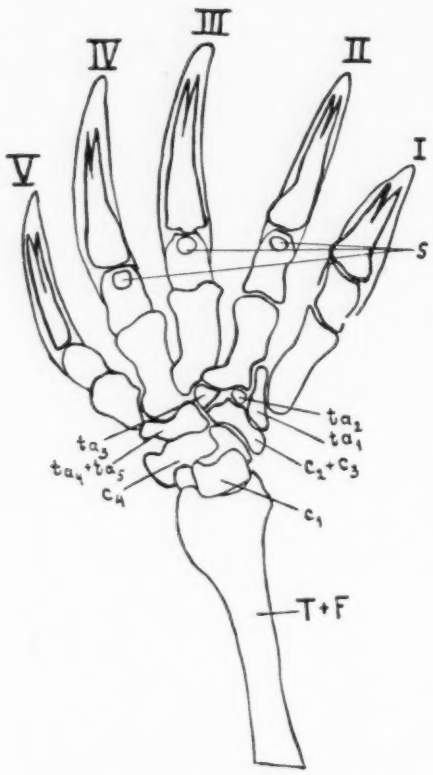

Fig. 18. Adult, foot from the dorsal side.

The metatarsal of the third toe is at its proximal end equipped with a side protuberance directed towards the fourth metatarsal.

Four tarsals exist, the fourth of which is more than twice as large as the rest and apparently composed of the tarsals 4 and 5. There is no longer any dividing line between its two components.

Central 1 (c_1) has grown considerably and is now a large cartilage rudiment at the distal end parts of the tibia and the fibula. A small blood-vessel passes through the cartilage. The fusion with the intermedium has probably taken place there (c_1+i).

Distally to central 1 the cartilage is situated, assumably a fussion of centrals 2 and 3 (c_2+c_3). This cartilage is now still more elongated than at the 10 mm stage. Towards the under-side of the foot it sends out a projection in a lateral direction past tarsal 1. As the structure of the projection and that of central 2+3 is different, it does not seem improbable that it might be the tibial that has fused with the central element.

Central 4 has grown. In the direction of the tibia a protuberance extends,

which comes into close contact with central 1. Between central 4 and the fibula a concentration of mesenchyme, viz, the fibular, is to be seen, which has a distinct connection with central 4.

The tibia has developed a fairly large projection in the distal direction.

At the latest of the embryonic stages, namely the 19 mm stage, the reduction of the number of skeleton parts has advanced further. The first and second phalanges in the second to the fifth toe have fused. A small canal, which passes through the whole of the compound cartilage, indicates the place of fusion. The cells lie arranged in two groups one on each side of the canal. Thus the phalanges of the foot show the same appearance as those of the hand. The number of phalanges is now the same in all the toes, though only two phalanges develop in the first. There, however, no fusion takes place.

The metatarsals I—IV are at their bases equipped with side-protuberances. Between metatarsals III, IV and V articulations have developed by means of the side-protuberances of the metatarsals III and IV.

Of the four tarsals the first and the fourth are the largest. The first has its length extension in a proximo-distal direction and is therefore driven up between metatarsals I and II. The last-mentioned cartilage articulates both with tarsals 2 and 3, because tarsal 2 is a fairly small cartilage and does not lie in a line with the distal edge of the tarsal row, but metatarsal II descends and comes into contact with tarsal 3. The fourth as well as the fifth metatarsal articulates with tarsal 4.

The proximal part of the tarsus has become narrower, the cartilages seem to have been pushed in the direction of the first toe. Central 2+3 is now much larger, and, as at the preceding stage, lies proximally to tarsals 1—3 with which it articulates. Tarsal 4+5 also comes into contact with central 2+3 and develops an articulation. It is no longer possible to see any dividing line at the lateral protuberance of central 2+3, mentioned at the preceding stage.

Central 4 has also grown considerably. Distally this cartilage articulates with tarsal 4+5, laterally with central 2+3 and central 1, and proximally with the fibula and the tibia. Apart from central 4, central 1 articulates with central 2+3, the fibula and the tibia. The last-mentioned two cartilages have fused distally and in doing so have contributed to making the proximal part of the tarsus narrower. Ossification is taking place in the central parts of the tibia and the fibula.

In full-grown animals the end phalanges of the toes are considerably extended, pointed, cleft and equipped with strong claws (figs. 18 and 19). At the articulations of the toes, sesamoids have developed (*s*). On the under-side of the foot these bones are to be found at the first as well as the second articulation. At the first articulation the sesamoids are as broad as the articulation itself; except those of the third toe, for which two smaller bones have been substituted At the second articulation all sesamoids are approximately

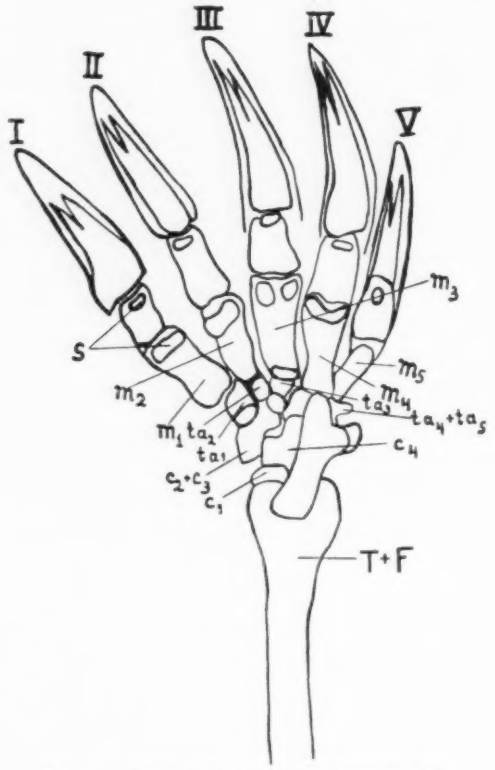

Fig. 19. Adult, foot from the palmar side.

equal and somewhat smaller than at the first articulation. On the upper side of the foot, on toes 2—4, there is a sesamoid immediately below the articulation (fig. 19). Thus both flexors and extensors have been reinforced with sesamoids.

The basal side-protuberances of metatarsals II—IV are strongly developed and all of them directed in one and the same direction (fig. 18). By means of these projections the foot is strengthened. Metatarsals I and II never come into contact with each other, because tarsal 1 is inserted between them. Thus metatarsal I only articulates with tarsal 1. Metatarsal II now articulates with tarsals 1—3 as well as with metatarsal III. Metatarsal IV now has an articulation with tarsal 3, without the articulations observed at the 19 mm stage.

SUMMARY.

Eremitalpa Granti was described for the first time in 1907 by BROOM. Already twenty years earlier the same author had discovered this species of the

Golden Mole. Eremitalpa Granti is the smallest species among hitherto known forms. That it was placed by ROBERTS in a special genus, in 1924, is due among other things to the fact that the fourth claw of the hand is comparatively well developed, which is not the case in any other genus. The descriptions of the structure of the extremities in Chrysochloris, which are to be found in the literature on the subject, apply to different species, but there are probably no important differences between the extremity skeletons of the various species.

CUVIER (1817), DESMAREST (1820), LESSON (1827), D'ALTON (1831), and others, were of the opinion that the hand in Chrysochloris has only three fingers. D'ALTON however adds "wenn wir uns nicht sehr trügen". On the outer side of the third finger D'ALTON found a small bone, having a protuberance which he took to be a sesamoid or a rudiment of the two missing fingers. MECKEL (1808) had earlier described four fingers in Sorex talpinus (Cape-mole), of which the outermost is directed downwards and is hardly visible. FISCHER (1829) also speaks of a tetradactylous hand. The presence of a fourth finger as described by MECKEL was, however, denied by D'ALTON, who considered this to be a projection on the articulation of the nail of the third finger. PETERS (1852) again demonstrated the presence of a small fourth finger.

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D'ALTON found seven bones in the carpus, arranged in two rows of four and three bones, respectively. According to DE BLAINVILLE (1839—64) one row consists of scaphoide, semilunare, triquetrum and pisiforme, and the other of trapèze, trapezoide and unciforme. Furthermore, the same author describes an intermediary bone between the scaphoide and trapèze. According to DE BLAINVILLE the carpus thus consists of eight bones. PETERS mentions only five, namely naviculare, semilunare and triquetrum in one row and capitatum and hamatum in the other. DOBSON (1883) calls these five bones scaphoideum, lunare and cuneiform in the first row and os magnum and unciform in the second. In DOBSON's figure and its explanation, besides the above-mentioned bones, also an ulnar sesamoid occurs, being situated laterally to the ulnar and proximally to the metacarpal IV.

The terms used in the present paper, which correspond to terms used by earlier authors, are given below:

naviculare	= scaphoideum	= radiale
semilunare	= lunare	= intermedium
triquetrum	= cuneiform	= ulnare
trapèze (ium)	= multangulum majus	= carpale 1
trapezoid	= „ minus	= „ 2
capitatum	= os magnum	= „ 3
hamatum	= unciform	= „ 4

In addition to the above-mentioned five bones in the carpus, also the os pisiforme is to be seen on the palmar side of the hand. I presume that the sesamoid which is mentioned in DOBSON's description constitutes the pisiforme.

That the number of bones in the hand becomes less during the animal's development was already suggested by D'ALTON. The bone to which the first and second fingers are articulated consists of a fusion of two bones, according to this author. PETERS has stated that the ossa multangula have either completely disappeared or have fused with the metacarpals of the first and second fingers. That these two bones are not present as independent bones was later confirmed by DOBSON among others, who calls them trapezium and trapezoid, and by CARLSSON (1903), who refers to them as multangulum majus and minus. The present investigation has shown that in the embryo carpals 1 and 2 are present as independent elements, but that in the course of development they fuse with one another and with metacarpal II. Thus, as PETERS has pointed out, metacarpal I does not articulate with metacarpal II, but, as is normally the case, with carpal 1, though this has fused with metacarpal II.

According to D'ALTON the first finger, which is the most developed, consists of a long metacarpal and two phalanges. PETERS says that the second finger also has two phalanges, but the third and fourth fingers have only one. D'ALTON has suggested that a fusion of metacarpal and phalange takes place in the second as well as in the third finger. The small fourth finger in Chrysochloris trevelyani has both a short basal phalange and one equipped with a nail, according to DOBSON. But in other species he has not found more than one phalange in the fourth finger. WINGE (1923) points out that the first and second phalanges of the second and the fourth finger have fused. In the third finger he maintains that all three phalanges have fused. But in my studies of embryonic stages I have been able to show that this is not the case, but that the first and second phalanges fuse with metacarpal III. The only phalange in the third finger is thus the third phalange.

The presence of sesamoids at the articulations of the fingers was already pointed out by D'ALTON.

In Eremitalpa Granti, the hand is so considerably changed, that it is impossible to trace the original type even in embryonic stages. No trace of any centrals has so far been observed at any developmental stage.

CUVIER states that the forearm is supported by a third bone, which lies under the elbow bone. According to PETERS, this constitutes a bone formation which forms part of the tendon of the flexor digitorum profundus muscle.

The foot is equipped with five toes, as was already shown by MECKEL and CUVIER. The tarsus is formed of seven bones and all five toes consist of two phalanges, the nail phalange being cleft in front, according to D'ALTON. Regarding the foot, WINGE writes that the first and second toe phalanges have fused. My investigations show that in Eremitalpa three phalanges are

formed in the second to the fifth toes, but that the first and second phalanges of these toes fuse in the course of development.

In the foot I have found four central elements. Central 1 fuses with the intermedium and forms the astragalus. Centrals 2 and 3 are united and form the naviculare, and central 4 fuses with the fibular and forms the calcaneus.

The theory founded by STEINER (1922) that four central elements originally exist in the carpus as well as in the tarsus in Tetrapodes has been further confirmed by the investigation of the foot of Eremitalpa.

Regarding Mammalia, HOLMGREN (1933) has shown four independent centrals in Mus, and I have found the same in embryos of Tarsius (1944), in the hand as well as in the foot. My investigations on Erinaceus (1941) and Talpa (1942) show the same conditions as in the foot of Eremitalpa, namely that centrals 2 and 3 are not distinctly separated from each other. In Elephantulus, Centetes, and Ericulus (1941), however, indications are present, which I have interpreted as signifying a junction of earlier separate elements.

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ABBREVIATIONS.

astr. astragalus.
c_1—c_4 centrals 1—4.
ca_1—ca_5 carpals 1—5.
cal. calcaneus.
cub. cuboideum.
F. Fibula.
f. fibular.
i. intermedium.
m_1—m_5 metacarpals 1—5 or metatarsals 1—5.
nav. naviculare.
pis. pisiforme.
ph. praehallux.
pm. postminimus.
pp. praepollex.
r. radial.
R. Radius.
s. sesamoids.
t. tibial.
T. Tibia.
ta_1—ta_5 tarsals 1—5.
u. ulnar.
U. Ulna.
1—3 phalangs.
I—V fingers or toes.

THE ONTOGENY OF THE LATERAL LINE SYSTEM IN THE HEAD OF DIPNOANS

BY

TORSTEN PEHRSON

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INTRODUCTION.

While the sensory line system in fossil Dipnoans in many important respects agrees with the conditions in *Crossopterygii,* as far as is known, it differs in several respects, in recent Dipnoans not only from what is met with in extinct Dipnoans, but, also from the conditions in other *Osteichthyes.*

The sensory line system often gives valuable intimations with phylogenetical relevancy, but, apart from the facts, firstly, that the main features of the line system in Dipnoans are in conformance with the pattern generally seen in Gnathostomes, and, secondly, that there are some special features, for instance the well-developed oral line which recalls conditions met with chiefly in the *Chondrichthyes,* the morphology of the line system in the adult gives few indications concerning the relationships of the Dipnoans.

Practically nothing is known about the ontogeny of the sensory line system in Dipnoans. GREIL's comprehensive treatise (1913) does not touch this problem except in one short notice which is vastly misleading, and also the line system in the adult has been the subject of comparatively few investigations (PARKER 1888, PINKUS 1895, KINGSBURY 1895, FÜRBRINGER 1904, GOODRICH 1925, 1930 and HOLMGREN 1942).

The deficiency in the knowledge of the ontogeny and the morphology of the lateral system in the head of Dipnoans has been observed especially by the palaeontologists. The investigation, the results of which are described in the present paper, might to a certain extent be said to have been induced by Professor E. Stensiö.

The material at hand has consisted of a complete series of developmental stages of *Neoceratodus (Epiceratodus) forsteri* from the length of 8.6 mm and upward, and of *Protopterus annectens* from the length of 10.0 mm and upward. The specimens have been sectioned in complete series of 8 μ thickness, except the large specimens where the thickness has amounted to 10 or 15 μ. The investigation has been carried out in the Zootomical Institute of the University of Stockholm.

The Protopterus material forms a part of the excellently fixed collections made by Dr Gustav S. O. Svensson during the Swedish Gambia expedition in 1932, the results of which, unfortunately, are still mainly unpublished due to the prolonged ill health of this eminent scientist. The *Neoceratodus* material has been collected and kindly put at disposal by the late Dr Thos. L. Bancroft, Eidsvold, Queensland.

The terminology used in this paper to denote the sensory lines is chiefly the one applied by Holmgren in his paper on the general morphology of the sensory line system in the head of fish (1942). Recently a comprehensive work by Stensiö (1947) has been published where new interpretations of the problems dealing with the morphology of the sensory line system in general are suggested. Stensiö's views will be dealt with in a treatise on the lateral line system, that will soon be published by N. Holmgren and the present author. They will not, therefore, be taken into consideration in this paper.

PROTOPTERUS ANNECTENS.

In all the youngest specimens the sensory lines have still placode shape and appear as continous ridges slightly raised above the surrounding epidermis, yet, not sufficiently so as to be distinguished in surface view. In the placode material the elongated primordia of the future neuromasts can be distinguished, but, as the sensory organ primordia pass one into another without distinct demarcation the placodes are represented in the figures showing the conditions in all the young specimens only as a continous ridge. In the 17.5 mm specimen the placodes begin to break up in distinct sense organs, and in a 19 mm specimen this process is practically finished.

The conditions in the youngest specimen of which a reconstruction could be made are represented in fig. 1, which shows one side of the head of a 10.1 mm specimen. The proximal portions of the supraorbital and the infra-

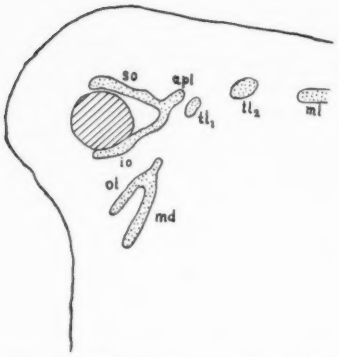

Fig. 1. *Protopterus,* 10.1 mm. Reconstruction, 25 ×. For letters, see p. 182.

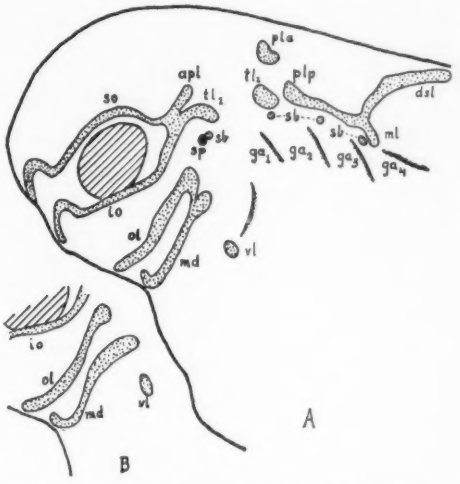

Fig. 2. *Protopterus,* 12.4 mm. Reconstruction, 25 ×. A, one side of the head. B, the oral and mandibular lines on the other side of the head. For letters, see p. 182.

orbital lines are formed as a V-shaped placode the sides of which enclose the eye from behind. On one side the anterior end of the temporal portion of the main body line is indicated as a short caudal prolongation. On the other side this portion forms as an independent patch (tl_1). This variability in the formation of the primordial elements of the sensory lines is extremely frequent not only in *Protopterus* but also in *Neoceratodus.* As a matter of fact it occurs only rarely that both sides of the head of a specimen agree in every detail of the line pattern, and a frequent type of variation is just that portions of the line system are formed either as independent patches or as appendages of already existing primordia.

A short dorso-caudal projection indicates the primordium of the future anterior head line of pits (*apl*).

Ventrally to the eye is another V-shaped placode, the common primordium of the oral and the mandibular lines. While the supra- and infraorbital placodes are innervated by the ramus ophtalmicus superficialis and the ramus buccalis respectively, this placode is innervated by the ramus hyoideo-mandibularis.

Still two lateralis placodes are developed at this stage, caudally to the eye, one anterior and one posterior. The latter is oblong and represents the anterior end of the vagus innervated main body line. The anterior placode is the primordium of the posterior, glossopharyngeus innervated portion of the temporal line (tl_2).

The position of the future spiracular organ cannot be observed with certainty at this early stage.

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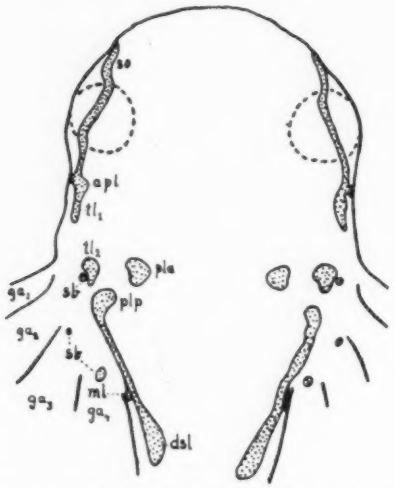

Fig. 3. *Protopterus*, 12.4 mm. Dorsal view of the head. Reconstruction, 25 ×. For letters, see p. 182.

In two 10.5 mm specimens the supraorbital line placode does not extend anterior to the middle of the eye. In a 10.7 mm specimen the distal end of this placode is still on a level with the middle of the eye. In a 11.0 mm specimen the placode has grown more rostrad and the typical loop of this portion of the line begins to show, although no connection between the right and the left line is attained.

At the next stage, a 12.4 mm specimen (figs. 2 and 3), the proximal end of the supraorbital and infraorbital placode is still V-shaped. Both lines have grown rostrad and attained the main course of the sensory lines in the adult. Anterior to the eye both lines run parallel. Before they turn ventro-caudad both make the dorsal loop so typical of the two lines in all following stages of development. On the ventral side of the snout the two supraorbital placodes meet to form a sort of cross commissure. Such is not the case with the distal ends of the two infraorbital lines. As HOLMGREN (1942) has pointed out a true ethmoid commissure formed by the infraorbital sensory lines does not exist in Dipnoans probably because of the moving ventrad of the nostrils.

From the common starting point of the supraorbital and the infraorbital lines, dorso-caudally to the eye, a short dorsal branch projects. It represents the future anterior head line of pits.

A projection caudad (tl_1) from the same point represents the anterior, oticus innervated end of the future temporal or cephalic portion of the lateral line. Still further caudad the posterior portion is represented, as at the previous stage, by a single placode (tl_2). The primordium of the main body line has grown rostrad and caudad. The rostral end is bent slightly rostro-dorsally and

will form the vestigial posterior portion of the posterior head line of pits. In the continuation caudad the placode line branches on a level with the last branchial arch. One short branch runs ventro-caudad and will form the anterior end of the main lateral line. The other branch runs in a dorso-caudal direction. The proximal portion will develop into the supra-temporal commissure whereas the distal portion represents the anterior end of the dorsal sensory line of the trunk (*dsl*).

The primordium of the posterior head line of pits is formed in two portions, one posterior and one anterior. The posterior portion (*plp*) consists of the anterior end of the vagus innervated placode whereas the anterior portion is represented by an isolated placode (*pla*) lying rostro-dorsally to the posterior portion. The position so far caudad and the near relation to the posterior portion make the supposition probable that the free placode is a portion of the posterior head line of pits. The homologisation will be confirmed by means of the innervation, at a later stage (p. 166).

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The once V-shaped common oral and mandibular line placode has also grown distad. At every stage of development of the sensory lines in *Protopterus* as well as in *Neoceratodus* there are variations which, probably, are of no morphological importance. One has already been pointed out (p. 155) and concerned the temporal portion of the main lateral line. A similar discrepancy is to be observed with regard to the oral-mandibular line placode: on one side (fig. 2 A) the placode is still V-shaped, but, on the other side (fig. 2 B) the dorsal ends have separated, and the two lines run almost parallel.

Ventro-caudally to the mandibular line another placode (*vl*) has developed at this stage. It is situated rostrally to the ventral corner of the gill cleft and is vagus innervated. It is the placode of the future ventral lateral line of the body.

At this stage the spiracular organ is easily discernible. It is situated antero-dorsally in the blind end of the spiracular cleft. The cells of the spiracular primordium, like those of the pharynx, are still filled with yolk granulae.

The primordium of a neuromast (*sb*) has formed in the epidermis outside the spiracular organ. This organ is, at this stage, connected with the spiracular organ by a string of epithelial cells. The organ is, contrary to the spiracular organ, only vestigial and disappears at later stages. It represents the most anterior organ in a rudimentary spiracular line, better developed in *Neoceratodus* larvae, as will be seen later on in this paper (p. 169). Similar vestigial organs have developed above the dorsal end of the three last branchial arches, thus, with the organ formed outside the spiracular organ included, forming a row of four sense organs. A similarly situated line of sense organs is described by HOLMGREN (1942) in Petromyzon where the neuromasts form a supra-branchial line. As far as the author knows, it is not described in any Gnathostome fishes.

The next stage is represented by a 13.6 mm specimen (figs. 4 and 5). The

general course of the supraorbital placode is the same as at the previous stage. Yet, there is one change which has to be observed. Immediately anterior to the eye is formed a short branch of the placode (fig. 4, *pet*). Further, there is rostrally to this branch a separate placode-like epithelial thickening in the epidermis. On the other side of the head of the specimen there are instead of one branch several short processes from the supraorbital line further caudad. In a 13.8 mm specimen the same rostral branch is to be seen on both sides and also in a 14 mm specimen (fig. 6, *pet*), although considerably reduced on one side where it is only represented by a small patch anterior to the portion of the supraorbital line which is situated rostrally to the eye.

HOLMGREN (1940, p. 76) has described a similar but larger and more differentiated epithelial thickening in the same place in a 22 mm *Squalus* embryo. According to HOLMGREN it does not differ, morphologically, in *Squalus* from the thickenings which develop into lateral line placodes, but, like the structure mentioned in *Protopterus* it disappears without giving rise to any definite organ. HOLMGREN suggests that, in *Squalus*, it may represent sensory line placodes, but rudimentary and "perhaps of distant phylogenetical importance". On the other hand, he says, it may indicate, judging from the position this part of the head will occupy in the adult, a method for the growth of the skin covering the brain. Although the present author is unable to form any theory as to the significance of the structure in question in *Protopterus*, the last-mentioned suggestion by HOLMGREN may seem less probable in this fish. The author, therefore, leaves the explanation of the structure to the future and is satisfied by pointing out the resemblance to the epithelial thickenings, in *Squalus*.

The infraorbital line offers nothing new in comparison with the previous stage. Because of the general growth in length of the head the posterior portion of the line has moved further caudad.

The most marked difference concerns the mandibular and also partly the oral lines. The oral line showed already at the previous stage a tendency to separate from the mandibular line. At this stage the separation is completed, but the line has neither grown in length nor altered its former position.

The dorsal portion of the mandibular line (fig. 4, *jl*) on the other hand has developed a marked loop caudad. This loop is connected with the infraorbital line. It will form the jugal line in the future line system.

The anterior end of the primordium of the cephalic portion of the lateral line remains at the same stage of development. Instead of an isolated placode which, at the previous stage, represented the middle portion of the cephalic line there are, on one side, two neuromasts (figs. 4 and 5, tl_2), on the other one. They indicate the future connection between the caudal end of the infraorbital line and the developing portion of the main lateral body line.

As to the future pit lines, the primordium of the anterior head line of

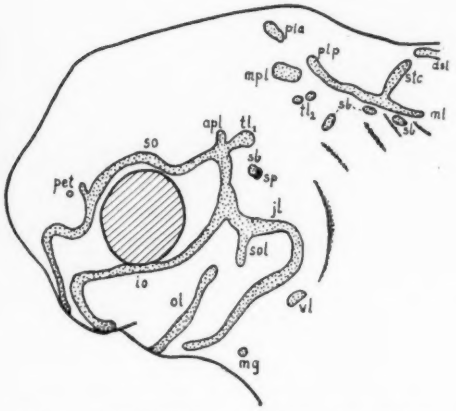

Fig. 4. *Protopterus*, 13.6 mm. Reconstruction, 25 ×. For letters, see p. 182.

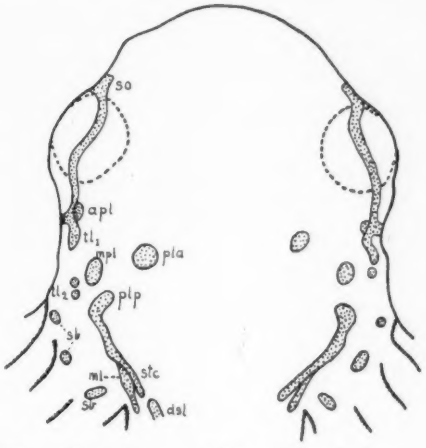

Fig. 5. *Protopterus*, 13.6 mm. Dorsal view of the head. Reconstruction, 25 ×. For letters, see p. 182.

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pits (*apl*) is still represented by a small outgrowth dorsally to the place where the supraorbital line and the postorbital portion of the infraorbital line meet.

The anterior portion of the posterior head line of pits (*pla*) has moved considerably rostrad, whereas the posterior portion (*plp*) is still attached to the primordium of the main body line.

Rostrally to this portion another placode (*mpl*) has formed. It is situated dorsally to the course of the temporal line. Yet, it can hardly belong to the posterior head line of pits as the development at the next following stages will show. It has to be interpreted as the primordium of the middle head line of pits.

A patch of thickened epithelium (*vl*) ventrally to the posterior end of the jugal loop represents the future ventral body line, and one caudally to the proximal end of the oral line is the primordium of the secondary oral line in the terminology used by HOLMGREN (1942). On one side (fig. 4, *sol*) this primordium is represented by a ventrad directed tongue-like outgrowth from the proximal end of the future jugal line. The primordium of the middle gular line (fig. 4, *mg*) appears on one side as a small patch posterior to the distal end of the mandibular line.

The vestigial suprabranchial line (*sb*) consists of the same number of sense organs as at the previous stage.

The 14 mm stage (figs. 6 and 7) does not differ in any important respects from the 13.6 mm stage. The projection from the supraorbital line anterior to the eye (*pet*), mentioned with regard to the 13.6 mm specimen (p. 158) is still visible. On one side it only consists of a small patch of cells but on the other side it has still the character of a dorsally directed process from the line.

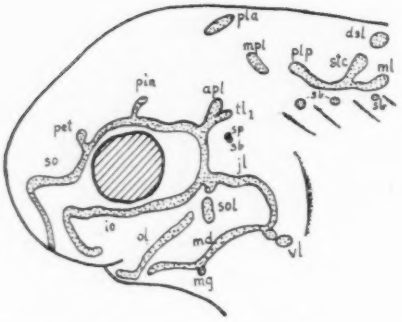

Fig. 6. *Protopterus*, 14 mm. Reconstruction, 25 ×. For letters, see p. 182.

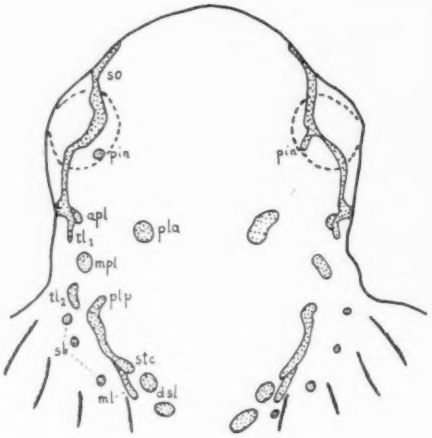

Fig. 7. *Protopterus*, 14 mm. Reconstruction, 25 ×. Dorsal view of the head. For letters, see p. 182.

The anterior end of the temporal line has grown a little further caudad, on one side removing with it the primordium of the anterior head line of pits which is still attached to it.

The dorsal end of the oral line has, now, fused with the infraorbital line on one side, but, is free on the other side (fig. 6) as at the previous stage. Because of the growth of the head the common loop of the jugal and the mandibular line extends still further caudad than at the previous stage.

As to the pit lines, the primordium of the anterior line, as mentioned above, is still attached to the infraorbital line on one side (fig. 6, *apl*). On the other side it forms a detached, separate placode.

The posterior head line of pits is developed as at the previous stage, the only difference being that the primordium of the anterior portion (*pla*) has moved further rostrad.

The placodes (fig. 7, *mpl*) rostrally to the posterior portion of the posterior head line and dorsally to the temporal line retain their former position. As pointed out before, they represent the primordia of the middle head lines of pits.

The secondary oral line is represented as at the previous stage on one side (fig. 6) by an isolated primordium, on the other by a ventro-rostrally directed process from the jugal line near its junction with the infraorbital line. At the same place on the opposite side of the head is a small vestige of this portion of the line.

Another vestigial line has developed at this stage. From the supraorbital line above the eye a short, dorso-caudally directed branch has formed on one side (*pin*). On the other side it is represented by an isolated patch. It is not an

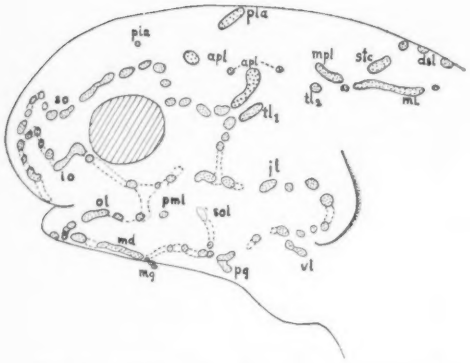

Fig. 8. *Protopterus,* 17.5 mm. Reconstruction, 20 ×. For letters, see p. 182.

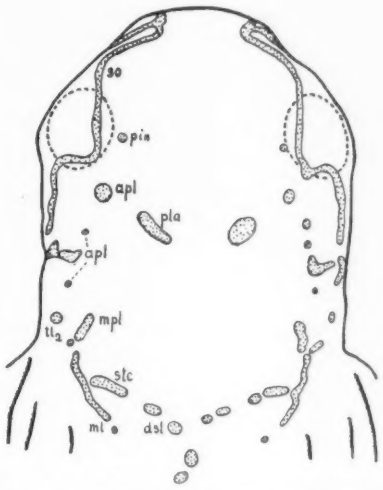

Fig. 9. *Protopterus,* 17.5 mm. Dorsal view of the head. Reconstruction, 20 ×. The supraorbital line schematically drawn. For letters, see p. 182.

occasional formation as it is seen at all stages between 14 and 18 mm. As it is situated so far rostrad it cannot be interpreted as the anterior head line of pits instead of the primordium situated further caudad that has been considered as this line. Besides, it disappears entirely at later stages. The only possible homology seems to be the pineal line, described by HOLMGREN (1942) in *Petromyzon,* Pteraspids and in Placoderms, such as *Coccosteus.* The final evidence, the trigeminal innervation, can not be given, however.

The primordia of the vestigial suprabranchial line are still developed as at the next youngest stage.

The primordium of the middle gular line (fig. 6, *mg*) is developed, at this stage, in the form of short ventro-caudally directed branches from the anterior portion of the mandibular line.

At the next stage, represented by a 17.5 mm specimen (figs. 8 and 9), the placodes which have, so far, been formed as continuous lines in the epidermis begin to break up and form distinct neuromasts. This refers to the future canal or groove lines as well as to the lines of pits. Yet, the formation of separate sense organs is not finished at this stage, and in several places there are still comparatively long portions of the lines where the character of a placode is still retained. In the majority of lines the sense organs are still connected by a line of epithelium, easy to distinguish from the surrounding epidermis. This specimen thus represents a distinct intermediary stage between the placode and the neuromast stage in the development.

As the figures show, the general pattern of the sensory line system agrees

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on the whole with what is seen at the previous stage. The most important change is that the dorsal end of the primary oral line (fig. 8, *ol*) has definitely fused with the infraorbital line. This fusion has apparently taken place considerably more distad than the connection which existed at earlier stages. Further, the loop of the jugo-mandibular line is prolonged still more caudad.

The primordium of the supratemporal commissure (*stc*) still remains as a branch of the main lateral line and is pointing dorso-caudad. In its prolongation caudad several free placodes are detached, representing the anterior end of the dorsal sensory line (*dsl*).

The middle gular line retains the former position, and, further caudad the primordium of the posterior gular line (*pg*) has developed. The secondary oral line still has placode shape. On one side it is attached with the dorsal end to the place where the jugal line fuses with the infraorbital line. On the other side (fig. 8) it is instead attached with its ventral end to the mandibular line immediately in front of the posterior gular line. The placode forms a connection between the infraorbital line and the mandibular line. In the adult the line runs in that way.

At the junction of the primary oral line and the infraorbital line the short primordium (fig. 8, *pml*) of another line of pits is formed. This is the future primary mandibular line in HOLMGREN's terminology (1942).

Of the head lines the anterior one (*apl*) is represented partly by an almost horizontal line consisting of several isolated patches or sense organs posterior to the most dorsal curve of the supraorbital line, partly by a vertical portion formed as a projection dorsad at the junction of the posterior end of the supraorbital line, the cephalic line and the infraorbital line. This projection, mentioned in the description of the previous stages, has grown still more dorsad, but retains it placode character so far. The horisontal portion consists of an anterior part and a short posterior part. The anterior line of pits as a whole has, thus, at this stage, the shape of a T. The anterior branch of the horizontal portion is on one side formed by three sense organs, on the other by two whereas the posterior branch only consists of one small sense organ (fig. 9). At next stage, a 19 mm specimen, the posterior branch of the line has disappeared. In *Protopterus annectens* the anterior head line of pits is formed, in the adult, only by an anterior horizontal and a vertical branch. In *P. aethiopicus* on the other hand this line has a T-shape. The conditions during the development of the line in *P. annectens* recall, thus, the conditions in the adult *P. aethiopicus*.

The middle head line of pits is more prolonged in a rostro-dorsal direction and begins to show signs of subdivision in isolated neuromasts.

As to the posterior head line of pits the anterior portion is represented by one placode on each side. On one side it is still rounded and rather large, on the other it is lengthened and shows the beginning of subdivision in neuromasts

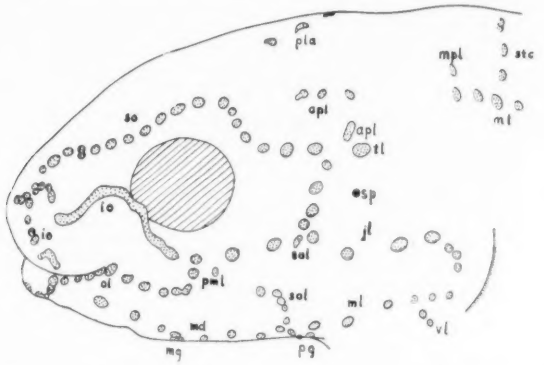

Fig. 10. *Protopterus*, 19 mm. Reconstruction, 25 ×. For letters, see p. 182.

(fig. 9). Both have moved still more rostrad and are now situated rostrodorsally to the dorsal end of the vertical portion of the anterior head line of pits. The primordium of the posterior portion of the posterior line of pits does not seem to develop any further, and is rather in a state of regression.

The primordium of the supratemporal commissure (*stc*) is now detached from the main line and has rotated so its direction is less caudal and more dorsal than before. Still further caudally the primordium of the anterior end of the dorsal sensory line is seen.

The suprabranchial line has now disappeared, but, the supposed "pineal" line is represented by one single little organ on each side above the eye.

In a 19 mm specimen (figs. 10 and 11) the placodes have almost entirely broken up into sense organs. The conditions at this stage are so reminiscent of the state in the adult that it is sufficient to point out the differences. The head has not yet attained the future proportions, as it is still much too short, comparatively.

The chief part of the temporal line is not formed so far. This line is only represented by one single neuromast at its anterior end. The supratemporal cross commissure consists of a row of four neuromasts on one side, three on the other (fig. 11) and has now attained its definite position straight across the head.

Immediately caudally to the middle of the supratemporal cross commissure the dorsal sensory line begins. Even the first organ in this line has now a dorsal position. The line continues caudad on each side of the dorsal fin fold whereas the main body line is discontinued immediately behind the few sense organs that show in the figures. It reappears considerably further back.

The pit lines of the head are still very short but show, generally, the conditions in the adult. The anterior head line only consists of an anterior horizontal portion and a vertical portion. The latter is formed by one single sense organ situated in the place where the first primordium developed, dorsally

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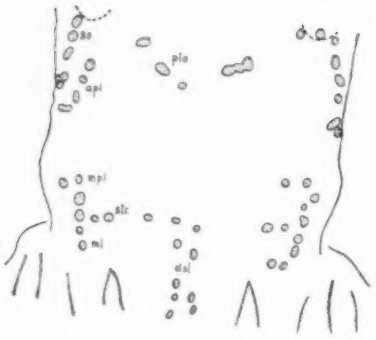

Fig. 11. *Protopterus*, 19 mm. Dorsal view of the head. Reconstruction, 18 ×. For letters, see p. 182.

Fig. 12. *Protopterus*, 21 mm. Dorsal view of the head. Reconstruction, 16 ×.

Fig. 13. *Protopterus*, 23 mm. Dorsal view of the head. Reconstruction, 20 ×.

to the postorbital portion of the infraorbital line. The horizontal part is developed on one side only and formed by three sense organs. On the other side only the vertical portion is seen (fig. 11).

As to the middle line, it consists of one or two sense organs. The anterior portion of the posterior line has advanced still more rostrad. On one side three separate neuromasts have formed, on the other there is an elongated placode just on the verge of breaking up into three sense organs (fig. 11). The posterior portion has, now, disappeared entirely. At this and the following stages the posterior head line of pits is represented only by the anterior portion.

In the angle posterior to the junction of the oral line and the infraorbital line the primary mandibular line is seen (fig. 10, *pml*), so far only represented by one single sense organ. Immediately ventrally to the angle between the infraorbital and the jugal lines are one or two isolated sense organs (*sol*). They represent the dorsal portion of the secondary oral line. This line develops late and is very short, also in the adult. Straight ventrally to these organs there is another line, formed by four or five sense organs. The dorsal end of this line is bent in a rostral direction and thus resembles the horizontally running secondary oral line in HOLMGREN's description of the conditions in the adult (1942, fig. 25). In a 17.5 mm *Protopterus* there is on one side, as mentioned above (p. 162), the primordium of a pit line emanating ventrad from the junction of the infraorbital and the jugal lines, thus indicating the course of the future secondary oral line. On the other side in the 17.5 mm specimen the primordium of this line is attached to the mandibular line straight ventrally to the place occupied by the line on the opposite side of the head. On the side where the primordium of the line emanates from the mandibular line the dorsal end of the primordium shows a faint curve rostrad (fig. 8).

Probably the horizontal line, according to HOLMGREN (1942) met with in some cases, is only the ventral part of the secondary oral line detached from

the dorsal end and bent rostrad. The vertical type of the line as well as the ventral, bent portion of the secondary oral line appear both as a continuation dorsad of the middle gular line at these old ontogenetic stages as well as in the adult. The occurrence of both types only indicates the variability of the line. As the development shows, the connection between the secondary oral line and the middle gular line is only secondary, the two lines originally developing as separate primordia, although their mutual positions in regard to the mandibular line alter later during the ontogeny.

The oldest specimen examined measured 55 mm in length (fig. 14). Here the head has attained the proportions of the adult and is considerably more elongated than earlier. There is nothing to add to the description of the line system, except that the temporal line is now completed because of the formation of new neuromasts.

As to the pit lines, the anterior pit line of the head has still the same shape and position as in the 19 mm specimen. The vertical portion is formed by two sense organs and the horizontal by five. The anterior end of the posterior line has grown ventrad and is thus situated rostrally to the anterior end of the anterior pit line. This bent vertical portion consists of five comparatively small sense organs which join the line formed by the previously four, now considerably larger organs.

The middle line has three or four organs.

The ontogeny of the posterior line seems to prove that it originates as two primordia as mentioned earlier, one attached to the anterior end of the primordium of the main body line, and one free placode, at the earliest stages situated close in front of this primordium (figs. 2 and 3). During the ontogeny this last-mentioned placode moves rostrad (figs. 5, 7, 9 and 11), and eventually reaches the position of what has been considered earlier the anterior head line of pits (fig. 14). No gap in the ontogeny seems to jeopardize this interpretation in spite of the fact that there is, from the late larval stages and upward, a considerable distance between the two portions of this line.

Further there is no doubt as to the homology of the anterior head line of pits when the ontogeny is taken into consideration. It is formed as mentioned, of two portions, one vertical and one horizontal, pointing rostrad. The only difficulty seems to be to fix the boundary between the distal ends of the anterior and the posterior lines, as the anterior portion of the former line is situated partly rostrally to the anterior head line and, apparently, forms a continuation of this line. In the 25 mm specimen this decision is very difficult to make, and already in a 30 mm specimen the distal ends of the two lines form one continuous row of sense organs. In a 21 mm specimen (fig. 12) the anterior line, however, is still very poorly developed, whereas the anterior end of the posterior line has formed a rostro-lateral curve. Yet, in a 23 mm specimen (fig. 13) the conditions seem to allow a safe distinction between the two lines. The

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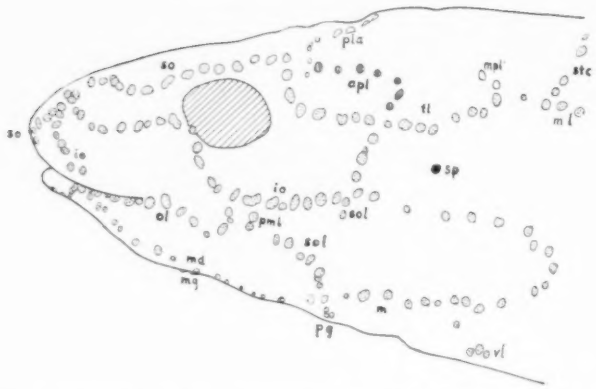

Fig. 14. *Protopterus*, 55 mm. Reconstruction, 13 ×. For letters, see p. 182.

anterior end of the posterior line has still the shape and course it has in a 21 mm specimen; even the number of neuromasts, 5—6, is the same, but, the horizontal portion of the anterior head line begins to develop in a rostral direction. It seems, to judge from the 23 mm specimen, that the anterior head line forms the horizontal portion only of the line system dorsally to the postorbital portion of the supraorbital line.

As to the posterior portion of the posterior head line of pits, it does not exist in the adult *Protopterus*. It appears as a primordium already at the 12.4 mm stage (figs. 2 and 3), can be traced at the next oldest stages up to the 17.5 mm stage (figs. 8 and 9), but, disappears later without leaving any traces. At this stage it has been possible to verify the homologisation of the head lines of pits by means of the innervation. In *Protopterus* there is a well developed nervus recurrens. The lateralis nerves are, however, independent, at least at the larval stages. It is comparatively easy to follow the innervation of the sense organs situated caudally to the trigemino-facialis ganglion.

The three anterior neuromasts shown in the temporal line in the reconstruction (fig. 14) are innervated by oticus branches and so is the spiracular organ. The three posterior sense organs in the temporal line are glossopharyngeus innervated. The organs forming what has been named in this paper the middle head line of pits also receive their nerves from a branch of the same nerve. This circumstance yields the final proof of the correctness of the homologisation of this line. As to the posterior head line of pits, at this stage situated partly medially, partly rostrally to the anterior head line of pits, it is innervated by a long nerve which runs in a curve along the side of the parietal region of the head eventually joining the vagus ganglion dorsally to the junction between this ganglion and the recurrens nerve. The sense organs in the supratemporal commissure are innervated, like the neuromasts still further caudad, by another lateralis nerve from the vagus ganglion.

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Considering the circumstances now related it does not seem probable that the homologisations of the pit lines on the head of *Protopterus* suggested by HOLMGREN (1942) are correct. What he calls the anterior line is chiefly the posterior line. His middle line corresponds, in the interpretation given above, to the anterior line and to the distal end of the posterior line, and his posterior line is the middle line.

The descriptions of the pit line system in *Protopterus* as well as that in *Neoceratodus* in earlier investigations are less detailed and not nearly as exact as HOLMGREN's because less importance was given to them. It is therefore of no value entering into detailed criticism of the data reported by earlier investigators.

The secondary oral line is formed, on both sides, by a short dorsal portion consisting on one side of two organs, on the other of only one. The ventral portion forms on both sides the same curve rostrad as was the case at the preceding stage. Ventrad it is continued by the posterior gular line. It is formed by six sense organs on each side.

The primary mandibular line (of HOLMGREN 1942) has two sense organs on each side.

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Results in Protopterus.

1. The first lines to develop are a) the supraorbital and the infraorbital lines, formed as a V-shaped placode consisting of the future proximal portions of the lines, b) the oral and the mandibular lines, also formed as a V-shaped placode, c) the main lateral body line, formed as an oblong placode caudally to d) the temporal or cephalic line which arises as one anterior (otic) placode and one posterior (glossopharyngeal) placode.
2. The distal ends of the supraorbital and the infraorbital lines develop very soon, the supraorbital lines on each side forming a commissure across the ethmoidal portion of the head whereas no infraorbital commissure develops.
3. The primordium of the oral line separates from the primordium of the mandibular line at early stages before the jugal line is formed, and later joins the infraorbital line. The dorsal end of the line seems to supply material for the formation of at least the dorsal portion of the secondary oral line.
4. A preopercular line does not form.
5. The jugal line develops as a curve caudad of the proximal portion of the jugo-mandibular line. In connection with the growth in length of the head, especially of the cheek region, the jugal curve forms the long loop caudad, typical of the adult.

6. The lines of pits develop either as isolated rounded placodes or as short branches from the canal lines placodes.
7. New interpretations are given to the head lines of pits. The three usual head lines of pits exist in *Protopterus*. The posterior line develops as an anterior and a posterior portion. The latter appears only as a vestigial primordium during some early larval stages.
8. A suprabranchial sensory line exists at some larval stages.
9. A "pineal" line is developed at some larval stages.
10. At some early developmental stages epithelial thickenings are formed connected with the anterior portion of the supraorbital line. They are, probably, homologous with similar growths found by HOLMGREN (1940) in early embryonic stages of *Squalus*.

NEOCERATODUS FORSTERI.

In *Neoceratodus* as in *Protopterus* the ontogeny of the sensory line system has been unknown, so far. In GREIL's treatise on the development of the head in *Neoceratodus* (1913) a short description of the sensory lines is given concerning one stage only (cf. p. 171).

The youngest stage which has been examined by the author is represented by a 8.6 mm specimen (fig. 15). The same elements of the sensory line system which formed the first primordia in *Protopterus* are also present in *Neoceratodus*, and the 8.6 mm specimen of *Neoceratodus* corresponds as far as the development of the line system is concerned very nearly to the 10.1 mm specimen in *Protopterus*. Contrary to the conditions at the youngest stage of *Protopterus*, however, the supraorbital and the infraorbital placodes are not joined. The supraorbital line has the shape of a short, straight horizontal placode, dorsally and dorso-caudally to the eye. The infraorbital line is represented by the portion situated ventrally to the posterior half of the eye, yet the placode continues straight caudad behind the eye. This part of the placode is the future temporal portion of the main lateral body line. In *Protopterus* the temporal line develops very late and is not represented by a continuous placode.

The common primordium of the oral and the mandibular lines is, as in *Protopterus*, represented by an inverted V-shaped placode which corresponds to the future proximal ends of the two lines.

At next stage, a 10.0 mm specimen (fig. 16), the supraorbital line has developed an anterior portion. Unlike the conditions in *Protopterus* it is not a direct continuation of the already formed proximal placode, but a new structure, separated from the anterior end of the proximal placode by a short space, also visible at the next following stages. The anterior portion of the supra-

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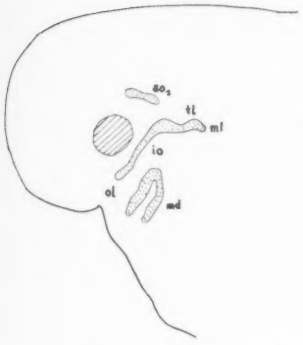

Fig. 15. *Neoceratodus*, 8.6 mm. Reconstruction, 25 ×. For letters, see p. 182.

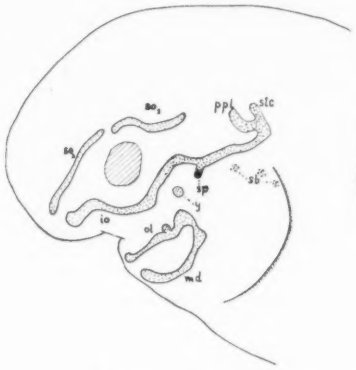

Fig. 16. *Neoceratodus*, 10 mm. Reconstruction, 25 ×. For letters, see p. 182.

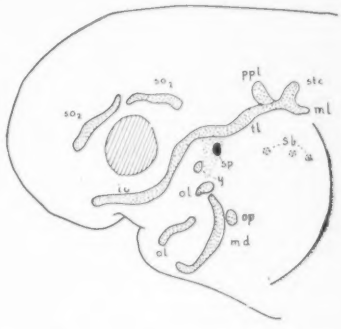

Fig. 17. *Neoceratodus*, 10.6 mm. Reconstruction, 25 ×. For letters, see p. 182.

orbital line is now longer than the proximal part, and reaches ventrally to the tip of the nose, yet, without forming, so far, an ethmoidal cross commissure.

The anterior end of the infraorbital line has also grown rostrad to a considerable extent. The temporal portion is similar to the previous stage.

The anterior portion of the main body line is also developed at this stage. A rostro-dorsally directed branch (*stc*) at the posterior end of the placode indicates the primordium of the supratemporal cross commissure.

Immediately rostrally to this branch there is another rostrodorsal branch (*ppl*). It is the origin of the posterior head line of pits. On one side this line is comparatively well-developed on the other it is only a short appendage at the base of the supratemporal commissure.

The spiracular organ in the vestigial spiracle slit has now developed. It is connected, as is the same organ in *Protopterus*, with a placode developed in the epidermis. In *Neoceratodus*, however, this placode has not the shape of a single patch, but, appears as a ventrally directed branch of the cephalic line. As in *Protopterus* it represents the anterior end of a suprabranchial or spiracular line. In *Neoceratodus* as in *Protopterus* there are also vestigial sense organs formed at the dorsal end of the branchial arches, forming a short line of three organs on each side. The well-developed operculum in *Neoceratodus* covers the line of three sense organs as the whole branchial region. The sense organs are not as well-developed as in *Protopterus*, where they are not covered by the operculum.

In a 10.6 mm specimen (fig. 17) the supraorbital line is still divided in an anterior and a posterior portion, the latter still being shorter. The infraorbital line forms one continous placode and also joins the primordium of the temporal portion of the main body line. The rostral end of the infraorbital line as well

as of the supraorbital line seem to be shorter at this stage than at the preceding one, judging from the position in relation to the eye.

The oral and the mandibular lines are still formed as a V-shaped common placode on one side. On the other the oral line is divided into one distal longer portion and one shorter, which is also free from the proximal end of the mandibular line (fig. 17). The mandibular line formed already at the preceding stage a slight curve caudad. At this stage this curve is more pronounced. It indicates the beginning of the formation of the jugal loop. Unlike the conditions in *Protopterus*, where the jugal line also develops as a curve in the mandibular line, but chiefly in the proximal portion of this line, the whole mandibular line in *Neoceratodus* seems to take part in the formation of this curve.

As to the pit lines on the head, there is still only the primordium of the posterior line to be seen. It is better developed than at the previous stage, and is separated from the supratemporal cross commissure primordium, but connected with the temporal portion of the main body line.

The spiracular organ is connected, by means of an epithelial strand, with an area of thickened epithel formed in the epidermis ventrally to the cephalic line and outside the locus of the spiracular organ. This area has not yet attained the character of a placode, but will give rise to one which will be seen at the next stage.

There are two placodes still to be mentioned. One is situated dorsally to the junction of the oral and the mandibular lines and rostro-ventrally to the place occupied by the spiracle. It will form the connection between the infraorbital and the future jugal line. In this specimen it is developed on one side only (fig. 17, *y*). On the other side it is indicated by a slight thickening in the epidermis on the inside, but is not visible from the surface. This placode can be observed at the previous stage (fig. 16, *y*). As to the possible homologies of this placode they will be discussed in a forthcoming paper by N. HOLMGREN and the present author, already mentioned (p. 154).

The other placode to be taken under consideration appears during the ontogeny but leaves, as far as is known, no trace in the adult. It is situated immediately posterior to the most caudal point of the mandibular line and has the shape either of a free patch-like organ or of a small appendage of the line (fig. 17, *op*). Although this organ disappears during later stages of the ontogeny it develops into organs which have considerably more resemblance to real sense organs than the cheek placodes. This placode is without doubt the homology of the short row of sense organs in *Protopterus*, posterior to the jugal canal (HOLMGREN 1942). Also in *Chlamydoselachus* there is a short prolongation of the jugal canal posterior to the point where the preopercular, the mandibular and the jugal canal meet in this fish, as is seen in fig. 1 in ALLIS's paper on this fish (1923). Neither HOLMGREN or ALLIS have given

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any name to this short line, for which the name opercular organs will be used in this paper.

As previously mentioned, pit lines arise ontogenetically in Dipnoans as rounded placodes, either isolated or in connection with other placodes. Later they give rise to one or several sense organs which change into a line of organs by means of division or budding of the first developed organ or organs. Placodes may also develop which do not change into sense organs, but disappear after a short temporary existence during the ontogeny. In Protopterus this is observed in several cases. These structures may give rise to several placode-like patches, but perish nevertheless without leaving a trace in the form of a permanent organ. Such placodes are to be considered as rudimentary organs, as vestigial primordia of sensory lines which have played a part in the phylogeny of the species but have disappeared. From such a point of view they may often be of great interest.[1]

GREIL (1913) shows in his figure 30 (fig. 18 in this paper), the lateral line system in a larval *Neoceratodus* at stage 44 in his description. GREIL does not mention the length of the specimens at this stage, but they were taken a week after hatching. At stage 45 where the larvae are two weeks after hatching their length is said, by GREIL, to be 11.5 mm. Judging from the shape and the stage of development as well as from GREIL's remark about the length of the stage 45 specimens, the 44 stage larva corresponds to about the 10.6 mm specimen dealt with above.

GREIL has studied the sensory line system in surface view. According to his description the thickened sensory lines in the epidermis of the head are plainly differentiated from the pigmented skin. The eye is surrounded dorsally and ventrally by the supra- and infraorbital lines. Both converge, GREIL says, towards the preotic resp. "prevestibular field" from whence they have taken their origin. From here runs, exactly opposite the first visceral pocket, the hyomandibular sensory line, the mandibular branch of which, still according to GREIL, does not stand out plainly in surface view. The same applies to the hypotic or intravestibular (temporal) line which runs caudad and is innervated by the lateralis system of the facialis as is the hyomandibular pharyngeal pocket organ (spiracular organ). At the dorsal connection of the operculum is situated, retrovestibularly, the centre of growth of the sensory stratum of the ectoderm from whence, except for the epibranchial thickenings of the ectoderm, the main sensory line of the body takes its origin. This line can already be traced towards the root of the tail. A branch of the retrovestibular sensory plate grows dorsad as the occipital line.

This is GREIL's description of the sensory canal system in the larva. As far as the words go, the difference does not seem to be great between GREIL's

[1] In a 22 and a 24.5 mm *Squalus* HOLMGREN (1940) has described a similar structure as a short caudal branch of the mandibular line.

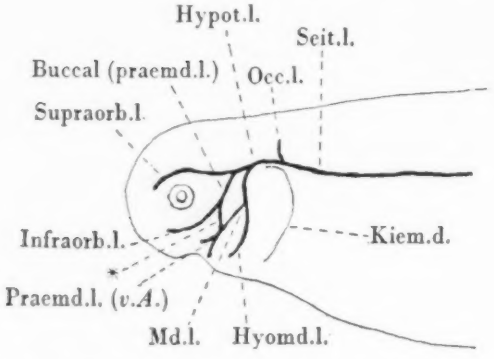

Fig. 18. *Neoceratodus*, embryo, stage 44. After Greil from Allis.

specimen and the 10.6 mm one described above. GREIL has illustrated his description with a figure which represents conditions rather far from reality (fig. 18). The probable explanation is that GREIL has interpreted pigment cells as sense organs. Anyhow, GREIL's figure has had a certain importance, as it has been the single document concerning the configuration of the sensory line system in the head of a larval Dipnoan. Various authors have studied the figure and founded more or less far-reaching discussions on its strange and unbelievable combination of lines.

It is useless to enter into a criticism of the details in GREIL's figure, it may suffice to refer to fig. 18 compared to fig. 17.

The next stage is represented by a 11.5 mm specimen (fig. 19) which corresponds to GREIL's stage 45. Several important changes in the developing sensory line system are to be observed in this specimen. One is that the placodes begin to dissolve into separate sense organs. Further there are characteristical changes in the course of almost all the lines, and finally it seems that the vestigial placodes or sense organs are better developed at this and the next following stages than at any other stage.

As to the supraorbital line the two separate placodes have fused on one side but not on the other. The rostral portion of the supraorbital line has grown more distad and reached its definite extension.

The infraorbital line has also grown rostrad. On the latero-ventral side of the snout where, at the next stage, the end of the infraorbital line meets the supraorbital line, the two line systems form an epithelial; thickened plate in which the elements of the two lines are impossible to distinguish from one another (fig. 20). A commissure between the two epithelial plates is to be assumed as being formed by the supraorbital lines, judging from the position in relation to the nostrils.

The temporal portion of the infraorbital line is partly dissolved in separate neuromasts.

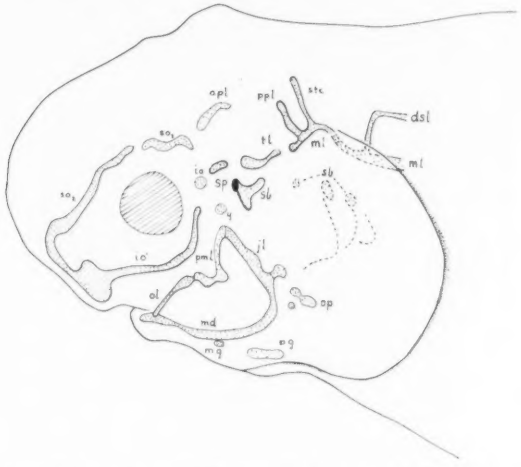

Fig. 19. *Neoceratodus,* 11.5 mm. Reconstruction, 25 ×. For letters, see p. 182.

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The primordium of the supratemporal cross-commissure is considerably prolonged in a rostro-dorsal direction.

The oral line is still apparently divided into a proximal and a distal portion. To judge from the conditions at the next stage, a 12 mm specimen, it seems, however, that the future oral line is only going to be formed by the distal portion. The proximal portion forms, at this stage, a right angle with the dorsal portion of the distal part which is bent in a caudal direction. On one side, the vertical side of the angle is broken off, but, on both sides, it maintains its original connection with the rostrad end of the jugal line. Judging from the conditions in the 12 mm specimen, this portion is, or forms, the primordium of the primary mandibular line and of the secondary oral line, according to HOLMGREN's terminology of 1942.

The caudal loop of the mandibular line is still more pronounced at this stage, and the result is that the division of the line into one ventral, chiefly horizontal mandibular portion (*md*), and one rostro-dorsally directed jugal portion (*jl*) can be distinguished.

The primordia of both the future head lines of pits are developed at this stage. Dorso-caudally to the posterior end of the supraorbital line is the primordium of the anterior head line of pits formed in the shape of a short independent placode (*apl*). This placode arises in the beginning as an independent structure, and, not as in *Protopterus,* in the shape of an appendage to the posterior end of the supraorbital line.

The primordium of the posterior head line of pits (*ppl*) already developed at the 10.0 mm stage as a short appendage anterior to the supratemporal commissure, is far better developed than at the preceding stages and stretches rostro-dorsad as a comparatively long branch from the anterior end of the

main body line placode. This pitline is called by HOLMGREN (1942) the middle line. As mentioned before (p. 157) the criterion of the homologisation of the head lines of pits is their innervation. In Dipnoans the occurrence of a nervus recurrens may make a reliable opinion concerning the provenance of the nerves disputable. In *Protopterus*, however, the independence of the lateralis nerves of the recurrens nerve makes an analysis of the innervation of the sense organs of the pit lines of the head comparatively easy and hence their homologisation.

In *Neoceratodus* the conditions are different. The glossopharyngeo-vagus ganglion is situated comparatively far back, posterior to the supratemporal cross commissure. The neuromasts of this line are innervated by a nerve branching off from the nervus recurrens on a level with this sensory line. From this nerve another branch is given off, innervating the sense organs in what has been called in this paper the posterior head line of pits. It is, under these circumstances, not possible to decide whether the pit line nerve in question contains vagus fibres or glossopharyngeus fibres or both kinds together, and the innervation does not give any clue to the homologisation.

The ontogeny of the line rather speaks in favour of the opinion that the line should be considered as a posterior line. It arises comparatively far back, as a matter of fact further back than is the case with the middle line in *Protopterus*. Moreover, in the adult it crosses the supratemporal cross commissure and may extend comparatively far caudad (cf. HOLMGREN 1942, fig. 24).

On the other hand the line is prolonged rostrad, considerably, at later larval stages. Possibly there are also elements of a middle head line of pits added to it. This might be considered probable as there is, in *Protopterus*, in the posterior parts of the parietal region of the head not only a middle head line of pits, hitherto considered as the posterior line, but, also, during early larval stages a vestigial posterior portion of a posterior head line of pits.

The primary mandibular line develops as mentioned above from the dorsal part of the common primordium of the oral and the mandibular lines. Also the secondary oral line seems to take its origin from the same source. This placode forms the apex of the rigth angle formed by the primordium of the primary mandibular line.

Ventrally to the caudal loop of the jugo-mandibular line, the placode of the gular line has developed. While *Protopterus* has two gular lines on each side, called the middle and the posterior gular lines by HOLMGREN (1942), the adult *Neoceratodus* has only one (cf. p. 179). This line is considered by HOLMGREN to be the homologue of the middle line. This primordium in the *Neoceratodus* larvae develops in the same place where the primordium of the posterior gular line forms in *Protopterus*, which seems to make it more probable that the single line in the description of the conditions in *Neoceratodus* actually is the homologue of the posterior line. This point of view is also

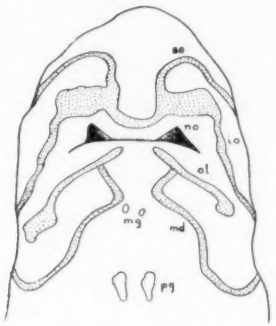

Fig. 20. *Neoceratodus*, 11.5 mm. Ventral view. Reconstruction, 25 ×. For letters, see p. 182.

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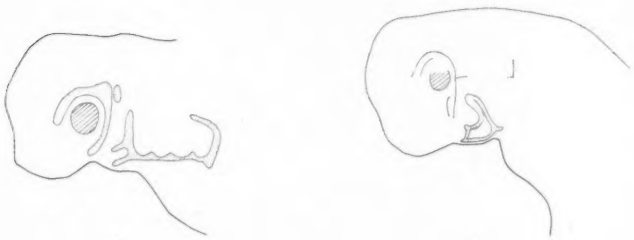

A. B.

Fig. 21. *Necturus*. A, embryo 13 mm, B, embryo 15 mm. Sensory line placodes, dotted fields; sensory lines, unbroken lines. After Platt.

supported by another fact. In the 11.5 mm specimen there is a small vestigial placode situated more rostrad, ventrally to the mandibular line, in the same place as the middle gular line in *Protopterus*. This placode can be followed at several later developmental stages, but, not in all. It is, thus, missing in the 14.5 mm specimen, but, still in the 43.5 mm specimen it is represented by a small abortive sense organ, visible only on one side of the jaw. This placode may, thus, be considered as a rudimentary middle gular line.

In the description of the 10.6 mm specimen a vestigial placode is mentioned posterior to the caudal loop of the jugo-mandibular line. It is the structure called the opercular organ (*op*) by the author. This organ has developed into several, of which one is formed as a short branch of the jugal canal. This structure is, as previously mentioned (p. 170), the homologue of the postjugal, short line sometimes developed in *Protopterus*. This suggestion applies at least to the dorsal elements found at this stage. The ventral element may correspond to the ventral lateral line developed in *Protopterus*.

On the cheek are two placodes. One is the placode marked (*y*), and already mentioned at the previous stage. The other is a comparatively large triangular

placode, connected with the spiracular organ by means of a strand of epithel. It is formed from the area of thickened epithel described in the 10.6 mm specimen. It is the homologue of the anterior end of the spiracular or supra-branchial line, described in *Protopterus* (p. 157). In the 10.0 mm specimen it is indicated as a short placode-like branch, connected dorsally with the temporal line and ventrally with the spiracular organ, situated in the rudiment of the spiracular cleft. In the 10.6 mm specimen this primordium corresponds to the area of thickened epithel, already mentioned and, in the 11.5 mm specimen, it has acquired the shape of an independent surface placode, though still connected with the spiracular organ. The primordium has shifted caudad in relation to the spiracular organ, probably because of the growth of the cheek region. The posterior portion of the line is still formed by the three vestigial sense organs at the dorsal end of the branchial arches, in *Neoceratodus* situated under the operculum and already described in the 10.0 mm specimen.

The arrangement of the primordia of the sensory lines in the 11.5 mm specimen of *Neoceratodus*, as previously described, offers a striking resemblance to the developing sensory line system in Urodeles, as it is represented in *Necturus* (PLATT 1896, fig. 21 in this paper). This chiefly concerns the lines still at the placode stage. When sensory organs are formed in *Necturus* they appear as longitudinal fields containing several rows of neuromasts. Hence the appearence of the proximal portion of the supraorbital and of the distal portion of the infraorbital lines which are doubled. The greatest resemblance to the conditions in the 11.5 mm *Neoceratodus* is found in the line pattern on the cheek. The oral and the jugo-mandibular lines diverge ventrad from a common apex, as in *Neoceratodus*. The oral line in *Necturus*, as in *Neoceratodus*, is divided into one dorsal and one ventral portion, of which the dorsal corresponds to the future dorsal portion of the primary mandibular line in *Neoceratodus*, whereas the ventral part is the homologue of the oral line. Where the jugal and the mandibular portions of the jugo-mandibular line meet, caudally, there is a short branch or appendage. If PLATT's figure of the 15 mm *Necturus* is compared with the 13 mm specimen (fig. 21 in this paper) it will be noticed that this small appendage is the remains of the long rostro-caudally running ventral ridge, better visible in the 12 mm *Necturus*.

In a 12.0 mm specimen (fig. 22) the placodes are mostly dissolved into separate neuromasts. Only in some places there are still placode fragments left, as for instance in the jugal line on both sides. On one side there is a short break in the supraorbital line indicating the dividing line between the anterior and the posterior portions of the original placode. At this stage the line system has attained the adult pattern on the whole, and the supraorbital and the infraorbital lines meet behind the eye. Yet, as the head still has the larval shortness, the distal portions of the supra- and infraorbital lines are

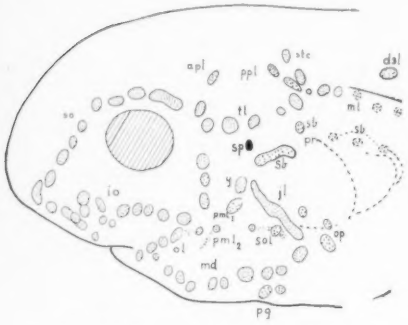

Fig. 22. *Neoceratodus*, 12 mm. Reconstruction, 25 ×. For letters, see p. 182.

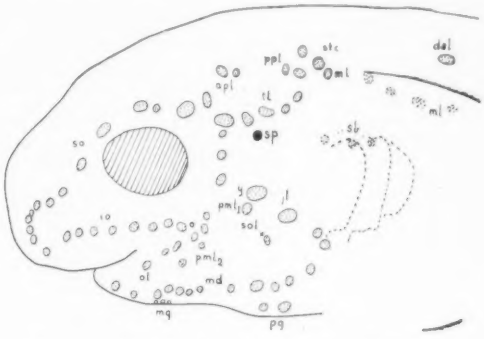

Fig. 23. *Neoceratodus*, 12.6 mm. Reconstruction, 25 ×. For letters, see p. 182.

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still limited to the ventral side of the snout. The shortness of the head is noticeable especially in the cheek region.

The temporal line has developed a row of neuromasts and is thus completed. The proximal end of the oral line has joined the infraorbital line (cf. p. 172). The loop of the jugo-mandibular line is still considerably shorter than in the adult. The jugal line seems to be the part of the line system which is furthest from completion. A comparatively great portion of the line still remains at the placode stage and the line is still running in a ventro-caudal direction.

The anterior pit line of the head has developed two neuromasts on one side, although not quite separated from each other, on the other side only one. The posterior line consists of two sense organs. The primary mandibular line is formed by two sense organs one dorsal and one ventral (fig. 22, pml_1 and pml_2). The secondary oral line has two sense organs on one side three on the other.

Only the posterior gular line is developed at this stage, and there is no sign of the vestigial middle line to be found. The posterior line is formed by two sense organs on each side.

There are three rudimentary opercular organs on each side as at the preceding stage.

As to the anterior end of the spiracular line, it consists now of two primordia, one anterior long and narrow placode, probably the remains of the large placode formed at the previous stage. Another small placode or sense organ has formed dorso-caudally. The three vestigial sense organs forming the posterior portion of the line still exist.

The next stage examined is represented by a 12.6 mm specimen (fig. 23). Here the remnants of the placodes, which were still left at the preceding stage, have dissolved into neuromasts. As far as the general course of the lines is concerned, there is nothing new to add, except that the distal ends of the

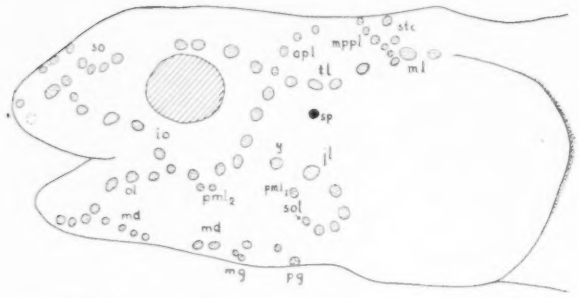

Fig. 24. *Neoceratodus*, 16.5 mm. Reconstruction, 20 ×. For letters see p. 182.

supraorbital and the infraorbital lines have shifted more onto the dorsal side of the snout. The jugal line has still the same slanting position as before because no considerable growth in length of the cheek region has taken place in the short interval between the 12.0 mm and the 12.6 mm stages.

As to the pit lines, it should be noticed that the vestigial suprabranchial line on the cheek has now disappeared. The same applies to the rudimentary opercular organs. On the other hand the middle gular line is preserved, and is formed by not less than three small sense organs while the posterior gular line consists of only two, though considerably larger sense organs. The three posterior suprabranchial organs also remain at this stage, but disappear later.

The remaining lines of pits have not altered to any great extent. The anterior head line of pits has three sense organs, and the posterior line as at the preceding stage two. The dorsal portion of the primary mandibular line and the secondary oral line are formed by one organ each. The ventral portion of the primary mandibular line consists of two sense organs.

The 16.5 mm stage (fig. 24) chiefly differs from the preceding one in the considerable growth in length of the head, consequently accompanied by a general stretching of the sensory lines as well. The jugal line begins at this stage to maintain a more horizontal position.

The pit lines on the head are lengthened by the development of additional sense organs, but, still maintain their original position. The anterior pit line has four sense organs and the posterior line five. On the other hand, the primary mandibular line and the secondary oral line are still only formed by two sense organs each. The middle gular line has two sense organs, and the posterior gular line only two in this specimen.

The oldest developmental stage examined is a five months old larva measuring 43.5 mm in length (fig. 25). Also here the changes in comparison with the nearest preceding stages are very few and chiefly concern the head lines of pits. The two head lines have developed so far that they meet. On one side they form a right angle on the other a curve. Yet, on both sides two interruptions suggest that the lines are formed by three different portions. As

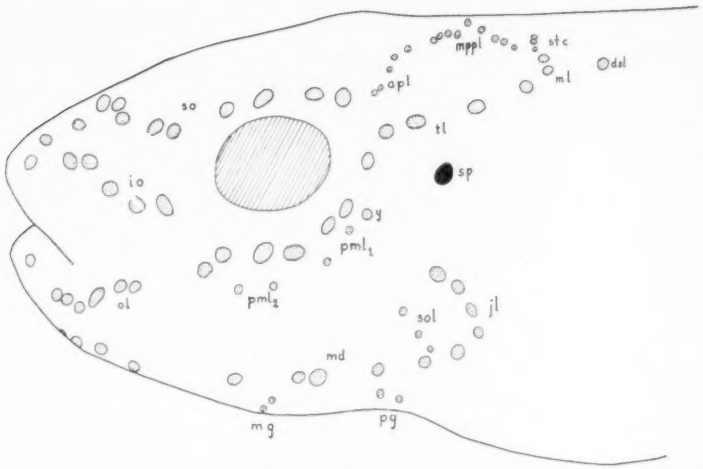

Fig. 25. *Neoceratodus*, 43.5 mm. Reconstruction, 11 ×. For letters, see p. 182

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has been pointed out in p. 174 in this paper, the so-called posterior line, probably, also contains elements of a middle head line of pits which develops comparatively late.

In a 2 1/4 years specimen the posterior line has changed its position slightly. Originally this line was formed as a branch of the anterior end of the main body line. At this stage the line has lost contact with the main line, and the posterior end now points towards the proximal portion of the supratemporal commissure slightly dorsally to the point where it fuses with the main dorsal line. Besides, the posterior line of pits crosses the supratemporal commissure and continues further caudad. This condition is indicated by the conditions in the 43.5 mm specimen.

The dorsal portion of the primary mandibular line consists of three sense organs one of which is the aforesaid organ termed *y*, and the ventral portion of two. The secondary oral line has three sense organs.

Finally it should be noticed that the middle gular pit line in this specimen consists of two neuromasts as does the posterior line. The author has had the opportunity of examining a 2 1/4 years old specimen more closely. Here the posterior gular line has turned into a line which crosses the space between the two mandibular lines. Further rostrad a short middle gular line is indicated as some isolated pit organs, situated where the so-called vestigial line is found in the young larvae. Also in three adult specimens of Ceratodus examined by the author there are, anteriorly to the posterior gular line, some irregularly spread isolated pit organs which obviously correspond to the middle pit line developed in *Protopterus*. The adult *Neoceratodus* may thus be said to posses at least a rudimentary middle gular line. In this connection it may also be mentioned that

the primordia of the gular lines in the young larvae (fig. 20) do not run transversally, but, together form a longitudinal line consisting of two short pieces on each side.

Results in Neoceratodus.

A summary of the most important features in the ontogeny of the latero-sensory lines in the head of *Neoceratodus* may be given as follows:

1. The origin of the primordia of the sensory lines takes place on the whole as in *Protopterus*, the chief differences as to the early stages being that a) the supraorbital line forms in two portions, one earlier posterior and one later anterior which fuse at about the period in the development when the isolated placodes begin to form neuromasts, b) the infraorbital line placode forms separated from the supraorbital, with which it does not become connected until separate neuromasts exist.
2. The middle head line of pits forms a portion of the posterior line.
3. A middle gular line develops during the ontogeny. In the adult it does not form a real gular line, but remains as scattered organs of pits.
4. During the ontogeny vestigial placodes form. They disappear before the end of the larval development and are interpreted as rudiments of phylogenetically important indices of lost sensory lines.

SUMMARY.

1. The first developing elements of the latero-sensory canals in the head of the Dipnoans examined are the placodes of the future supra- and infraorbital lines, the placodes of the oral and jugomandibular lines, and, slightly later, the primordium of the anterior end of the main body line. The oral and jugo-mandibular lines form as a common V-shaped placode in *Protopterus* and *Neoceratodus*, the supraorbital and infraorbital lines also as a V-shaped placode, but, only in *Protopterus*.
2. No preopercular line is formed either in *Protopterus* or in *Neoceratodus*.
3. The jugal line develops from the dorsal half of the jugalo-mandibular line, but other elements as well take part in the formation of this line, at least in *Neoceratodus*.
4. In *Protopterus* as well as in *Neoceratodus* vestigial sensory lines develop during the ontogeny which disappear without leaving traces, as a spiracular or suprabranchial line in *Protopterus* and in *Neoceratodus*, the posterior portion of the posterior head line of pits in *Protopterus* and the opercular line in *Neoceratodus*.
5. New interpretations are given to the head lines of pits in *Protopterus* and *Neoceratodus*.

6. The developing sensory line system in the head of the examined Dipnoans recalls on one hand the conditions in Selachians on the other those in Amphibians (*Necturus*).

The author has not been able, so far, to survey the bearings of the ontogenetical results on phylogenetical problems. Since GREIL's misleading statements have now been removed the knowledge of the ontogeny of the sensory lines in Dipnoans may be of great importance for a discussion not only of the sensory line system on the whole, but, also of more general phylogenetical problems.

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ABBREVIATIONS.

apl anterior head line of pits.
dsl dorsal sensory line.
ga gill arch.
io infraorbital line.
jl jugal line.
md mandibular line.
mg middle gular line.
ml main body line.
mpl middle head line of pits.
no nostril.
ol oral line.
op opercular sense organs.
pct placode-like epithelial thickening in the supraorbital line.
pg posterior gular line.
pin "pineal" line.
pla anterior portion of posterior head line of pits.
plp posterior portion of the same.
pml primary mandibular line.
pml_1 dorsal portion of mandibular line.
pml_2 ventral portion of mandibular line.
ppl posterior head line of pits.
sb suprabranchial sense organs.
so supraorbital line.
so_1 posterior portion of supraorbital line.
so_2 anterior portion of supraorbital line.
sol secondary oral line.
sp spiracle organ.
stc supratemporal cross commissure.
tl temporal portion of main lateral line.
tl_1 anterior part of temporal portion of main lateral line.
tl_2 posterior part of temporal portion of main lateral line.
vl ventral lateral line.
y placode connecting jugal and infraorbital lines.

PRIMI RISULTATI SULL'AZIONE DELL'ACETATO DI DESOSSICORTICOSTERONE SULLO SVILUPPO DELLE GONADI NELL'EMBRIONE DI POLLO [1]

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INTRODUZIONE.

Recentemente il PADOA (1943) ha dimostrato che un ormone sintetico della corteccia surrenale, l'acetato di desossicorticosterone, ha effetto femminizzante sulle gonadi dei girini delle rane. Subito dopo io ho rilevato che tale effetto può essere attribuito al fatto che il desossicorticosterone inibisce lo sviluppo della porzione midollare, potenzialmente testicolare, della gonade: se il trattamento viene iniziato molto presto, le gonadi dei girini risultano costituite quasi esclusivamente dalla porzione corticale, potenzialmente ovarica, e perciò sono capaci di differenziarsi soltanto in direzione femminile (VANNINI 1944).

L'attività femminizzante dell'ormone corticosurrenale sembra dunque differente da quella dell'ormone follicolare dell'ovaio (estradiolo), che femminizza le gonadi senza ostacolare l'iniziale sviluppo del tessuto midollare, ma favorendo l'accrescimento prevalente della porzione corticale e il differenziamento ovocitario degli elementi germinali in questa contenuti. Per indicare questi diversi meccanismi dell'effetto femminizzante dei due ormoni steroidi, ho chiamato

[1] Il presente lavoro è stato effettuato con un sussidio del Consiglio Nazionale delle Ricerche.

azione medullo-inibitrice quella del desossicorticosterone, e *azione cortico-stimolatrice* quella dell'estradiolo (VANNINI 1945 b, 1946) [1].

In ricerche successive ho messo in evidenza, sempre nei girini delle rane, che anche gli effetti mascolinizzanti dell'ormone testicolare (testosterone) e dell'ormone del corpo luteo (progesterone) si esplicano con un meccanismo differente [2]. Mentre, infatti, il testosterone mascolinizza gli abbozzi delle gonadi stimolando l'accrescimento del tessuto midollare, il progesterone raggiunge il medesimo effetto terminale ostacolando la formazione degli ovociti nella cortex. Se il trattamento con testosterone o con progesterone viene effettuato sulle ovaie di girini in iniziale metamorfosi, il primo effetto del testosterone consiste nel riempimento delle cavità centrali delle ovaie da parte di un abbondante tessuto midollare di nuova proliferazione, e solo in seguito nella regione corticale, invasa da tale tessuto neoformato, si assiste ad una degenerazione degli ovociti, completante la mascolinizzazione delle ovaie; nelle medesime condizioni, il primo effetto del progesterone consiste invece in una rapida degenerazione degli ovociti contenuti nella cortex, e solo in seguito (quando tutti gli ovociti sono ormai distrutti) si verifica una proliferazione di tessuto midollare, che riempie le cavità entovariche e conduce alla genesi di testicoli normali. Si può dunque affermare che gli effetti mascolinizzanti sono dovuti ad un'*azione medullo-stimolatrice* per il testosterone, e ad un'*azione cortico-inibitrice* per il progesterone (VANNINI 1947 a).

Questi reperti, dimostranti una così marcata differenza fra le azioni dei quattro tipi principali di ormoni steroidi, mi sembra rappresentino un progresso nelle nostre conoscenze sui fenomeni di inversione sessuale ormonica sperimentale. Anche se l'inevitabile schematismo delle prime conclusioni potrà forse essere in parte modificati da indagini future [3], l'avere rilevato come possano ottenersi mascolinizzazioni o femminizzazioni per un'azione stimolatrice o inibitrice sui territori corticale o midollare delle gonadi, utilizzando ormoni steroidi dell'adulto, induce a ritenere assai probabile che sostanze appartenenti alla medesima categoria chimica possano intervenire nei processi spontanei della

[1] Ultimamente il PADOA (1947) ha mosso qualche dubbio sull'affermata diversità di azione fra estradiolo e desossicorticosterone. Ricerche in corso confermano però le mie asserzioni.

[2] L'effetto mascolinizzante del progesterone sulle gonadi dei girini delle rane è stato scoperto circa contemporaneamente dal PADOA (1943) e dal PARDINI (1943), che hanno sperimentato su girini di *Rana esculenta* L. Le mie ricerche sono state effettuate su girini di *Rana dalmatina* Bp. (sin. *R. agilis* Thom.).

[3] Mi riferisco al fatto che uno stesso ormone può esercitare, a dosi differenti, effetti opposti sul differenziamento sessuale delle gonadi. Nei girini delle rane, tale fenomeno è stato chiaramente dimostrato dal PADOA (1943) per l'estradiolo, che in basse dosi svolge il normale effetto femminizzante, mentre in dosi elevate mostra un effetto «paradossale» mascolinizzante. E' assai probabile che anche altri ormoni steroidi possano svolgere azioni multiple sulle gonadi dei girini delle rane: ricerche in corso, finora pubblicate solo parzialmente in via preliminare (VANNINI 1947 c), mostrano per esempio che il desossicorticosterone, per lo meno in date dosi, esplica, accanto ad un'intensa azione medullo-inibitrice, una più blanda azione inibitrice sullo sviluppo degli elementi germinali nella cortex.

differenziazione sessuale. Le conoscenze attuali sulla determinazione sessuale, non solo negli Anfibi, ma anche nei Vertebrati ad essi superiori (cfr. WITSCHI 1934, 1942), mostrano infatti chiaramente l'intervento, nei processi di sviluppo e di differenziamento delle gonadi, di sostanze a tipo ormonico(espressione dell'attività del patrimonio genetico individuale), le quali vengono secrete dalla cortex e dalla medulla dell'abbozzo della gonade (cortessina e medullarina + e — del WITSCHI), ed esercitano le medesime azioni stimolatrici e inibitrici, da me viste per gli ormoni steroidi sperimentati [1]. In questo senso, i miei reperti sulle azioni degli ormoni steroidi nella gonade degli Anfibi sono stati citati e utilizzati dal WOLFF (1947 a), in un recente tentativo d'interpretazione dei risultati di moderni esperimenti d'intersessualità ormonica nei Vertebrati.

Questa sommaria ricapitolazione dei precedenti risultati sugli Anfibi era necessaria, per comprendere le ragioni che mi hanno spinto alla indagine sulla quale attualmente riferisco [2]. Con i presenti esperimenti, intendo infatti iniziari una serie di ricerche, dirette a rilevare se anche nell'embrione degli Uccelli i vari ormoni steroidi agiscano in maniera paragonabile a quella descritta per i girini delle rane.

Esperimenti notissimi sull'embrione di pollo, di WILLIER, WOLFF, DANTSCHAKOFF e altri studiosi più recenti, hanno mostrato, fin dal 1935, che nell'abbozzo delle gonadi l'estradiolo, l'estrone ed altri estrogeni hanno un effetto femminizzante, mentre gli androgeni, e soprattutto il testosterone, agiscono mascolinizzando. Tali risultati vengono raggiunti con un meccanismo identico a quello rilevato per gli Anfibi, perchè gli estrogeni stimolano l'accrescimento della porzione corticale, ed il testosterone stimola lo sviluppo della porzione midollare della gonade [3].

Per gli embrioni degli Uccelli, finora non erano stati descritti gli effetti del progesterone e degli ormoni steroidi della corteccia surrenale sul differenziamento sessuale delle gonadi. L'indagine presente costituisce dunque un primo tentativo di colmare questa lacuna, limitatamente però al desossicorticosterone, che si considera uno dei più attivi fra gli ormoni della corteccia surrenale.

[1] Per maggiori dettagli su queste assomiglianze di azione sugli Anfibi, vedi VANNINI 1947 a.

[2] I principali risultati del presente studio sono stati già esposti, in via preliminare, in una breve nota riassuntiva (VANNINI 1947 b).

[3] La copiosa bibliografia sull'argomento è rintracciabile, per la massima parte, nei lavori più estesi e comprensivi di V. DANTSCHAKOFF (1941), B. H. WILLIER (1942) ed E. WOLFF (1946, 1947 a). Possiamo inoltre citare, fra i più recenti, uno studio di Boss e WITSCHI (1947), che, iniettando stilbestrolo in uova di *Larus argentatus*, hanno ottenuto femminizzazione delle gonadi maschili; ed una relazione preliminare di NAESLUND (1947), sui risultati di iniezioni di estrone e di testosterone nell'uovo di pollo. Non è per me necessario entrare qui in dettagli più precisi: basterà perciò accennare al fatto che, nell'embrione di pollo, gli ormoni androgeni sono assai meno efficaci e più nocivi che gli estrogeni; taluni androgeni (androsterone, deidroandrosterone) mostrano inoltre, accanto alla loro azione mascolinizzante sulle ovaie, anche un'azione «paradossale» femminizzante sui testicoli.

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IMPOSTAZIONE E METODICA DEGLI ESPERIMENTI.

L'impostazione sperimentale è stata guidata dalla conoscenza, da me acquisita in ricerche precedenti (VANNINI 1943, 1945 a), dello sviluppo delle gonadi nel pollo.

In condizioni normali, nell'embrione di pollo, la parte corticale delle gonadi — costituita da un ispessimento della parete peritoneale contenente le cellule germinali primordiali — compare, sotto forma di cresta genitale, fin dallo stadio di circa 36 ore di incubazione. Il tessuto midollare comincia a svilupparsi nell'interno delle gonadi all'età di 4 giorni e mezzo; esso proviene dagli abbozzi del tessuto interrenale, in accordo con quanto si verifica anche nei girini degli Anfibi (VANNINI 1942). Fino allo stadio di 5 giorni di incubazione, il tessuto midollare delle gonadi e gli abbozzi del tessuto interrenale appaiono fra loro in diretta continuazione, e il progressivo accrescimento del tessuto midollare dipende essenzialmente da una continua penetrazione di elementi interrenali entro l'abbozzo delle gonadi. Solo all'età di 5 giorni e mezzo, e più ancora a quella di 6 giorni di incubazione, tali connessioni di tessuti si interrompono, onde a partire da queste fasi dello sviluppo l'abbozzo interrenale non fornisce più nessuna cellula alla medulla delle gonadi, il cui ulteriore accrescimento perciò dipende solamente da attività mitotiche degli elementi che la costituiscono.

All'età di 6 giorni di incubazione, gli embrioni di pollo hanno dunque gonadi sessualmente indifferenziate e bipotenti, nelle quali sono ormai abbozzate definitivamente sia la porzione corticale, potenzialmente ovarica, che la porzione midollare, potenzialmente testicolare; le cellule germinali primordiali sono contenute quasi esclusivamente nella prima di queste due porzioni della gonade. Il successivo differenziamento sessuale, che dovrà verificarsi in ulteriori stadi, avverrà in direzione femminile se prevarrà l'ulteriore sviluppo della cortex, e in direzione maschile se viceversa prevarrà l'accrescimento della medulla. Le cellule germinali primordiali diverranno gonociti femminili se conserveranno la loro primitiva localizzazione nella cortex; invece diverranno gonociti maschili, se si sposteranno in seno al tessuto midollare della gonade (DANTSCHAKOFF 1941, WITSCHI 1935).

In questa prima serie di esperimenti orientativi, non ho studiato l'azione dell'acetato di desossicorticosterone sul vero e proprio differenziamento sessuale delle gonadi; ma ho voluto, per ora, limitarmi a esaminare *se un precoce trattamento con l'ormone della corteccia surrenale riesce a modificare la quantità di tessuto midollare che si sviluppa nell'interno delle gonadi* di embrioni che non oltrepassano il 6° giorno di incubazione, e che perciò sono ancora sessualmente indifferenziati. In previsione che il desossicorticosterone potesse agire nel pollo in modo simile a quanto ho già descritto per gli Anfibi — ostacolando cioè lo sviluppo del tessuto midollare della gonade, senza però distrug-

gere l'eventuale tessuto midollare già formato—, ho ritenuto opportuno sottoporre al trattamento sperimentale embrioni di pollo appartenenti a stadi assai iniziali. Ho scelto infatti l'età di 48 ore di incubazione, alla quale non si è ancora formata neppure la porzione corticale dell'abbozzo della gonade; in tal maniera tutto il periodo della genesi del tessuto midollare delle gonadi ha potuto svolgersi in presenza dell'ormone della corteccia surrenale.

Ho adoperato l'acetato di desossicorticosterone, prodotto dalla casa Ciba e messo in vendita con il nome commerciale di Percorten [1]. Questa sostanza, ottenuta per sintesi allo stato cristallino, era sciolta in olio di sesamo alla concentrazione del 5 $^0/_{00}$; tale soluzione oleosa veniva da me introdotta, in una sola volta, entro l'albume di uova poste ad incubare da 48 ore. L'iniezione è stata sempre effettuata attraverso un piccolo forellino praticato nel guscio dell'uovo in corrispondenza del polo ottuso; l'ago della siringa veniva introdotto molto obliquamente, per una profondità di circa 2 cm, con una orientazione tale da garantire contro eventuali lesioni della membrana vitellina. Prima di praticare il forellino, il guscio dell'uovo veniva sterilizzato sul polo ottuso con una soluzione satura acquosa di acido picrico. Dopo l'inezione ormonica, il forellino praticato nel guscio veniva richiuso con una goccia di paraffina fusa, e l'uovo veniva nuovamente posto ad incubare.

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La quantità di acetato di desossicorticosterone iniettato fu per alcune uova di mg 0,5, per altre di mg 1 e per altre ancora di mg 2. Dosi più alte non vennero impiegate, perchè in alcuni tentativi si dimostrarono costantemente letali. Ma anche le dosi da 0,5 a 2 mg non apparvero innocue per gli embrioni di pollo. Infatti, su 5 embrioni trattati con 0,5 mg ne sopravvissero 3; su 18 embrioni trattati con 1 mg ne sopravvissero 6; e su 9 embrioni trattati con 2 mg ne sopravvissero soltanto 2. La tossicità dell'acetato di desossicorticosterone va dunque progressivamente crescendo con l'aumentare della dose. Gli embrioni sopravvissuti al trattamento apparivano esteriormente normali.

La maggior parte delle uova iniettate sono state aperte all'età di 6 giorni di incubazione; altre uova invece sono state aperte alle età di 4 giorni e mezzo, 5 giorni e 5 giorni e mezzo, che corrispondono a fasi diverse dello sviluppo della porzione midollare delle gonadi. All'epoca dell'apertura delle uova, gli embrioni trovati vivi sono stati fissati in liquido di Bouin, inclusi in paraffina e sezionati in serie, in fette trasversali di 10 μ, per l'esame istologico della regione delle gonadi. Le fette sono state colorate con ematossilina-eosina.

Le gonadi degli embrioni trattati con acetato di desossicorticosterone sono state confrontate con gonadi di embrioni normali di controllo, della stessa età, fissati sezionati e colorati nell'identica maniera.

[1] Colgo l'occasione per esprimere la mia riconoscenza alla Società Ciba, che anche questa volta mi ha generosamente fornito in omaggio l'ormone necessario agli esperimenti.

DESCRIZIONE DEI RISULTATI.

Dall'esame dei preparati istologici degli esemplari uccisi all'età di 6 giorni di incubazione, è apparso subito evidente che le gonadi degli embrioni trattati con desossicorticosterone sono nettamente più piccole che quelle degli embrioni normali di controllo, e che tale ipoplasia dipende prevalentemente da un minor volume della regione midollare; la riduzione volumetrica è tanto più notevole, quanto maggiore è la dose di ormone adoperata.

Desiderando valutare con maggiore precisione i risultati ottenuti, ho ritenuto necessario ricorrere però ad un'analisi quantitativa. Questa è stata realizzata proiettando l'immagine, ingrandita 540 volte, delle fette trasversali delle gonadi e disegnando con esattezza, per ciascuna di esse, i confini delle regioni corticale e midollare. Dato il notevole numero di fette di ogni gonade, è risultato superfluo ed eccessivamente laborioso eseguire su tutte le fette la descritta operazione; è apparso, invece, più che sufficiente disegnarne una ogni cinque. Con un planimetro, sono state poi accuratamente calcolate le superfici delle regioni corticale e midollare di ogni fetta, e le somme delle superfici delle varie fette di ogni gonade sono state assunte come un indice dei rispettivi volumi complessivi.

Tali calcoli sono stati effettuati separatamente per le gonadi destra e sinistra, sia negli embrioni di controllo che in quelli trattati con acetato di desossicorticosterone. I valori relativi così ottenuti sono riportati nelle annesse Tabelle I e II, nelle quali vengono pure indicate le lunghezze delle gonadi (ricavate dal numero delle loro fette trasversali di 10 μ), i valori corrispondenti ai loro volumi complessivi, e i volumi percentuali della regione midollare, riferiti ai volumi complessivi di ogni gonade. I numeri d'ordine degli embrioni corrispondono a quelli dei protocolli degli esperimenti.

TABELLA I.

Embrioni di pollo di 6 giorni di età, normali o ormonizzati. Valori riguardanti la gonade sinistra.

No. d'ordine degli embrioni	Trattamento	Lunghezza della gonade in mm	Volume della cortex	Volume della medulla	Volume complessivo della gonade	Volume percentuale della medulla
18	Controllo	1,49	573,5	2.258,5	2.832,0	79,8 %
17	„	1,19	586,5	1.504,5	2.091,0	72,0 %
6	„	1,40	600,5	1.250,5	1.851,0	67,6 %
42	0,5 mg di ormone	1,23	616,5	1.811,0	2.427,5	74,6 %
4	„	1,57	645,5	1.170,5	1.816,0	64,5 %
10	„	1,51	507,5	747,5	1.255,0	59,6 %
13	1 mg di ormone	1,22	320,0	624,0	944,0	66,1 %
8	„	1,17	300,0	429,5	729,5	58,9 %
9	„	1,06	281,0	382,0	663,0	57,6 %
11	2 mg di ormone	1,10	345,0	345,5	690,5	50,1 %
39	„	1,26	289,5	340,0	629,5	54,0 %

TABELLA II.

Embrioni di pollo di 6 giorni di età, normali o ormonizzati. Valori riguardanti la gonade destra.

No. d'ordine degli embrioni	Trattamento	Lunghezza della gonade in mm	Volume della cortex	Volume della medulla	Volume complessivo della gonade	Volume percentuale della medulla
18	Controllo	1,36	325,5	1.709,5	2.035,0	84,0 %
17	„	1,08	218,0	725,5	943,5	76,9 %
6	„	1,39	314,0	1.158,5	1.472,5	78,7 %
42	0,5 mg di ormone	1,39	306,0	1.651,0	1.957,0	84,4 %
4	„	1,40	292,5	992,5	1.285,0	77,2 %
10	„	1,07	127,5	463,0	590,5	78,4 %
13	1 mg di ormone	0,93	95,0	470,5	565,5	83,2 %
8	„	0,75	86,0	234,0	320,0	73,1 %
9	„	0,46	53,0	166,0	219,0	75,8 %
11	2 mg di ormone	0,61	70,5	163,0	233,5	69,8 %
39	„	1,00	82,5	220,5	303,0	72,8 %

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Dal confronto dei valori delle tabelle, appare pienamente confermata l'impressione che si ricavava dal semplice esame microscopico.

Per quanto riguarda la lunghezza delle gonadi, è evidente che questa risulta leggermente diminuita, rispetto agli embrioni normali di controllo, nei trattamenti con 1 o con 2 mg di acetato di desossicorticosterone, mentre non mostra modificazioni significative nei trattamenti con 0,5 mg. Le diminuzioni di lunghezza sono un po' più intense per la gonade destra, che, come è noto, negli embrioni degli Uccelli è normalmente di volume ridotto rispetto alla gonade sinistra.

Ben più cospicue sono però le modificazioni di volume delle gonadi, per indicare le quali ho costruito, in base ai dati delle Tabelle I e II, gli istogrammi delle fig. 1 e 2. Nonostante il numero relativamente piccolo di embrioni esaminati e la cospicua variabilità individuale nella grandezza delle gonadi, rilevabile anche negli embrioni normali di controllo, è assai evidente che l'acetato di desossicorticosterone provoca una diminuzione di volume negli abbozzi delle gonadi, non molto intensa nei trattamenti con 0,5 mg, ma assai marcata in quelli con 1 mg e soprattutto con 2 mg di ormone.

Possiamo infatti calcolare che, in media, in confronto al volume delle gonadi normali di controllo, il volume della gonade sinistra è diminuito del 19 % nei trattamenti con 0,5 mg, del 66 % nei trattamenti con 1 mg, e del 71 % nei trattamenti con 2 mg di acetato di desossicorticosterone; per la gonade destra, le rispettive diminuzioni medie di volume sono invece del 14 %, del 76 % e dell' 82 %. In accordo con quanto è stato rilevato per le diminuzioni di lunghezza, alle dosi di 1 e di 2 mg di acetato di desossicorticosterone la diminuzione di volume della gonade è un po' più forte a destra che a sinistra.

Soprattutto però interessa valutare *in qual misura le due porzioni costitutive della gonade partecipino alla descritta riduzione di volume*. Gli istogrammi delle fig. 1 e 2 sono appunto costruiti in modo tale, da agevolare la soluzione di

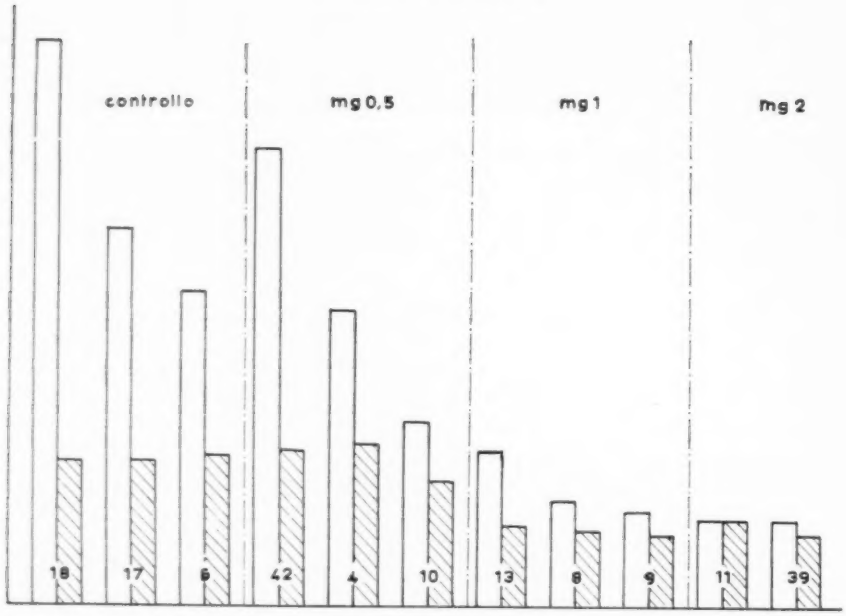

Fig. 1. Diagramma rappresentante l'effetto dell'acetato di desossicorticosterone sullo sviluppo della gonade sinistra negli embrioni di pollo. Ogni coppia di istogrammi corrisponde al volume complessivo della gonade di un embrione dell'età di 6 giorni di incubazione: gli istogrammi tratteggiati esprimono il volume della porzione corticale, quelli bianchi il volume della porzione midollare della gonade. I numeri alla base di ogni coppia di istogrammi sono i numeri di protocollo dei rispettivi embrioni. La prima parte del diagramma si riferisce agli embrioni normali di controllo; le altre parti agli embrioni trattati con 0,5 mg, 1 mg e 2 mg di acetato di desossicorticosterone.

questo problema. Essi, infatti, permettono immediatamente di apprezzare che nella gonade sinistra degli esemplari trattati con desossicorticosterone la riduzione di grandezza è dovuta prevalentemente ad una diminuzione di volume del territorio midollare; la porzione corticale delle gonadi partecipa in misura molto più ridotta al processo di ipoplasia sperimentale (fig. 1). Dai dati della Tabella I possiamo calcolare che in media, nella gonade sinistra, il volume della porzione midollare è diminuito, in confronto agli esemplari di controllo, del 26 % nei trattamenti con 0,5 mg, del 72 % in quelli con 1 mg e dell' 80 % in quelli con 2 mg di acetato di desossicorticosterone; la porzione corticale della gonade ha invece conservato approssimativamente il volume normale nei trattamenti con 0,5 mg, ed ha subìto una diminuzione di volume soltanto del 49 % nei trattamenti con 1 mg e del 46 % in quelli con 2 mg di ormone della corteccia surrenale.

Effetti simili, ma condizioni un po' diverse, si riscontrano per la gonade destra, che negli esemplari normali di controllo è provvista di una regione corticale atrofica, di volume molto scarso. Nei trattamenti con 0,5 mg o con 1 mg di acetato di desossicorticosterone, non si rileva una netta differenza fra

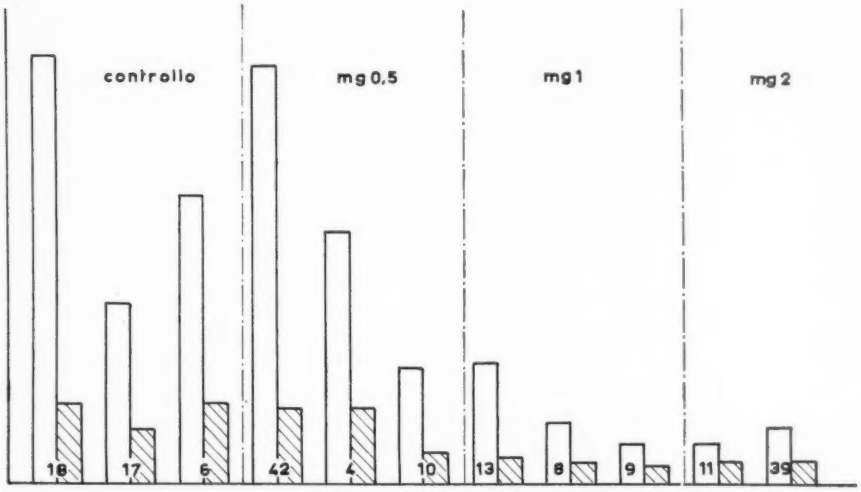

Fig. 2. Diagramma rappresentante l'effetto dell'acetato di desossicorticosterone sullo sviluppo della gonade destra negli embrioni di pollo. Per le altre spiegazioni, vedi la didascalia della figura precedente.

l'intensità della diminuzione di volume nella medulla e nella cortex della gonade; nei trattamenti con 2 mg di ormone, la diminuzione di volume della medulla è solo leggermente più intensa che la diminuzione di volume della cortex (fig. 2). In media, nella gonade destra, il volume della porzione midollare è diminuito, in confronto agli embrioni di controllo, del 13 % nei trattamenti con 0,5 mg, del 76 % in quelli con 1 mg e dell' 84 % in quelli con 2 mg di acetato di desossicorticosterone; per la porzione corticale della gonade, le rispettive diminuzioni medie di volume sono state del 16 %, del 73 % e del 74 %.

Possiamo anche rilevare che il comportamento delle gonadi destre dei singoli esemplari, di fronte al trattamento sperimentale, sembra meno regolare che quello delle gonadi sinistre; forse ciò può essere messo in relazione con la notevole variabilità individuale, che presentano i volumi delle gonadi destre anche in normali condizioni di sviluppo.

Considerando le gonadi sinistre nei vari embrioni studiati, possiamo constatare che, in confronto al volume complessivo di ogni singola gonade, il volume relativo della rispettiva porzione midollare diminuisce progressivamente nei trattamenti con dosi crescenti di ormone della corteccia surrenale (Tabella I). E' questa un'evidente conseguenza degli effetti ormonici descritti. Mentre negli esemplari normali il volume del tessuto midollare corrisponde, in media, al 73 % del volume complessivo della gonade, tale volume percentuale medio della medulla si riduce al 66 % nei trattamenti con 0,5 mg di acetato di desossicorticosterone, al 61 % in quelli con 1 mg e al 52 % in quelli con 2 mg. Naturalmente, a questa progressiva diminuzione del volume relativo del territorio midollare corrisponde un progressivo aumento del volume relativo della por-

zione corticale della gonade; sebbene il trattamento con acetato di desossicorticosterone faccia diminuire i valori volumetrici assoluti sia della cortex che della medulla, si ottengono dunque gonadi sinistre provviste di una quantità relativa di cortex più elevata del normale.

Anche nella gonade destra si verifica il medesimo fenomeno, meno intenso però, perchè la cortex destra, già normalmente ipoplasica negli embrioni di controllo, viene inibita dal desossicorticosterone più fortemente che quella sinistra. Come risulta dai dati della Tabella II, a destra il volume relativo del tessuto midollare, riferito al volume complessivo della gonade, è in media dello 80 % sia negli esemplari di controllo che in quelli trattati con 0,5 mg di ormone; è invece del 77 % nei trattamenti con 1 mg e del 71 % in quelli con 2 mg.

In conseguenza del diverso grado di reattività delle due gonadi di ciascun embrione, il trattamento con acetato di desossicorticosterone provoca evidenti modificazioni anche nel rapporto fra le dimensioni delle gonadi di destra e di sinistra. Malgrado la notevole variabilità individuale, riscontrabile anche negli embrioni di controllo, risulta chiaro dai valori della Tabella III che le differenze relative di lunghezza e di volume fra le gonadi destra e sinistra (già piuttosto elevate negli embrioni normali) aumentano sensibilmente nei trattamenti con 1 mg o con 2 mg di ormone della corteccia surrenale.

Tale accresciuta differenza di grandezza tra le due gonadi di ciascun embrione è legata soprattutto ad un aumento delle differenze relative fra i volumi della cortex di destra e di sinistra; solo in misura molto minore essa è dovuta anche a un aumento della differenza di volume fra le regioni midollari dei due lati. Già negli embrioni normali, le gonadi destra e sinistra differiscono fra loro maggiormente per l'estensione della cortex che della medulla: il trattamento con acetato di desossicorticosterone accentua tale condizione, poichè, come vedemmo, questo ormone inibisce lo sviluppo della porzione corticale più fortemente a destra che a sinistra.

TABELLA III.

Embrioni di pollo di 6 giorni di età, normali o ormonizzati. Rapporti fra le dimensioni delle gonadi destra e sinistra di ciascun embrione.

No. d'ordine degli embrioni	Trattamento	Rapporto fra le lunghezze delle gonadi	Rapporto fra i volumi delle gonadi	Rapporto fra i volumi della cortex	Rapporto fra i volumi della medulla
18	Controllo	0,91	0,71	0,56	0,75
17	„	0,90	0,45	0,37	0,48
6	„	0,99	0,79	0,52	0,92
42	0,5 mg di ormone	1,13	0,80	0,49	0,91
4	„	0,89	0,70	0,45	0,84
10	„	0,70	0,47	0,25	0,61
13	1 mg di ormone	0,76	0,59	0,29	0,75
8	„	0,64	0,43	0,28	0,54
9	„	0,43	0,33	0,18	0,43
11	2 mg di ormone	0,55	0,33	0,20	0,47
39	„	0,79	0,48	0,28	0,64

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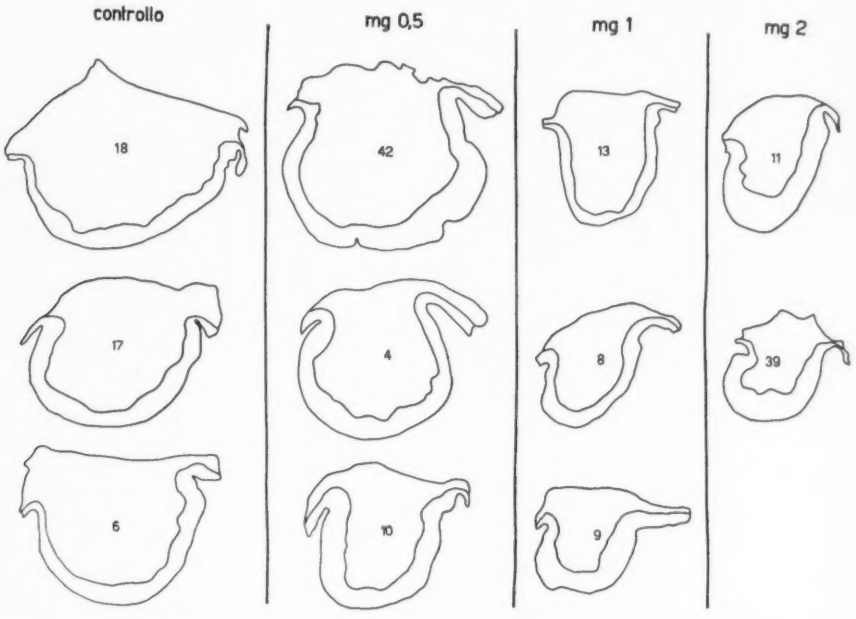

Fig. 3. Aspetto delle sezioni trasversali delle gonadi sinistre negli embrioni normali o ormonizzati, dell'età di 6 giorni di incubazione. Per ogni gonade è stata disegnata le fetta trasversale maggiormente estesa. L'orlo inferiore di ciascuna gonade rappresenta la sua porzione corticale; il rimanente territorio è la porzione midollare. I numeri contenuti entro ciascuna gonade sono quelli di protocollo dei singoli embrioni. Nella prima colonna sono contenute le gonadi degli embrioni normali di controllo; nelle colonne rimanenti sono invece comprese le gonadi degli esemplari sottoposti a trattamento con 0,5 mg, 1 mg o 2 mg di acetato di desossicorticosterone. Tutte le gonadi, originariamente disegnate all'ingrandimento 540 ×, sono state ridotte, per la stampa, all'ingrandimento di 110 ×.

Per completare la documentazione dei miei risultati, riporto nelle fig. 3 e 4 una serie di disegni, ognuno dei quali rappresenta la più estesa fra le sezioni trasversali dell'intera gonade, destra o sinistra, di ciascuno degli embrioni di 6 giorni di età da me studiati. Tali disegni sono stati scelti fra quelli adoperati per il calcolo dei volumi delle gonadi, e vi sono indicate separatamente le estensioni delle porzioni corticale e midollare: confrontando queste estensioni negli esemplari di controllo e trattati sperimentalmente, è possibile valutare l'attività esplicata sulle gonadi dall'acetato di desossicorticosterone. Nelle fig. 5 e 6 riporto infine la riproduzione fotografica della regione delle gonadi di un esemplare normale e di uno trattato sperimentalmente; per entrambi gli embrioni è stata scelta una sezione trasversale attraversante le gonadi nel loro tratto più voluminoso, onde permettere che, anche qui, il confronto delle due fotografie renda conto dell'intensità degli effetti esercitati dall'ormone della corteccia surrenale.

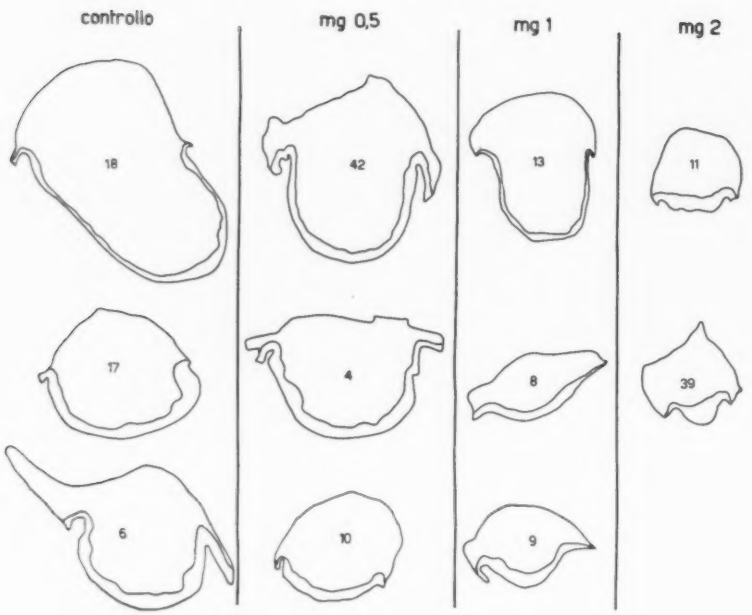

Fig. 4. Aspetto delle sezioni trasversali delle gonadi destre negli embrioni normali o ormonizzati, dell'età di 6 giorni di incubazione. Per le rimanenti spiegazioni, vedi la didascalia della figura precedente.

I risultati fin qui raggiunti, ricavati dall'esame di embrioni uccisi all'età di 6 giorni di incubazione, mi hanno invogliato a effettuare una seconda serie di osservazioni, nelle quali ho adoperato embrioni trattati nell'identica maniera di quelli precedenti, ma uccisi in stadi più precoci.

Il mio scopo è stato quello di vedere in che modo venga raggiunta la descritta ipoplasia delle gonadi, riguardante soprattutto il volume della regione midollare. Come abbiamo già detto, lo sviluppo di questo territorio delle gonadi ha il suo inizio all'età di 4 giorni e mezzo di incubazione, e continua fino all'età di 5 giorni per diretta derivazione dagli abbozzi interrenali; già all'età di 5 giorni e mezzo le connessioni fra tessuto interrenale e tessuto midollare delle gonadi cominciano a interrompersi, e perciò a partire da questo stadio di sviluppo l'ulteriore accrescimento della medulla delle gonadi continua a effettuarsi soltanto per mitosi delle cellule che la costituiscono. Mi è sembrato sufficiente esaminare un embrione ormonizzato per ciascuno dei tre suddetti stadi di sviluppo e, per confronto, altrettanti embrioni normali di controllo della medesima età. La dose di acetato di desossicorticosterone, adoperata in questo gruppo di esperimenti, è stata quella di 1 mg, inoculata entro l'uovo, come al solito, all'età di 2 giorni di incubazione; tale dose, come abbiamo dimostrato, è già

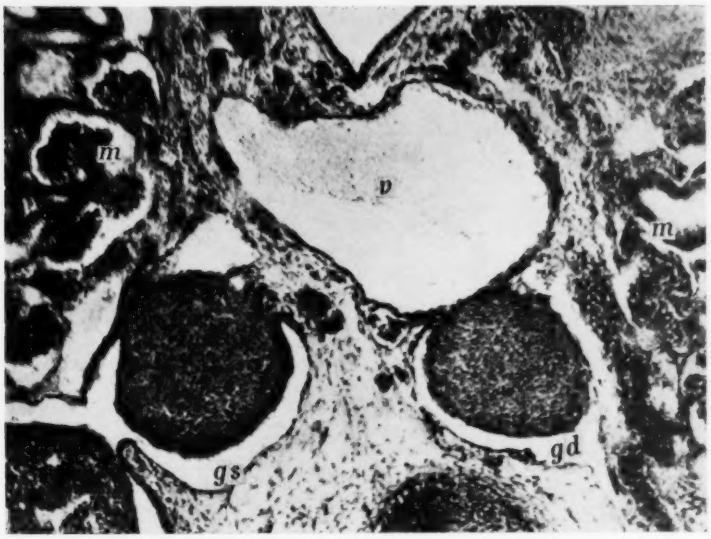

Fig. 5. Dalla sezione trasversale di un embrione normale di controllo, ucciso all'età di 6 giorni di incubazione (esemplare no. 17); la sezione è stata praticata al livello della massima dimensione delle gonadi. *gd* gonade destra; *gs* gonade sinistra; *m* mesonefro; *v* vena cava posteriore. Ingrandimento 130 ×.

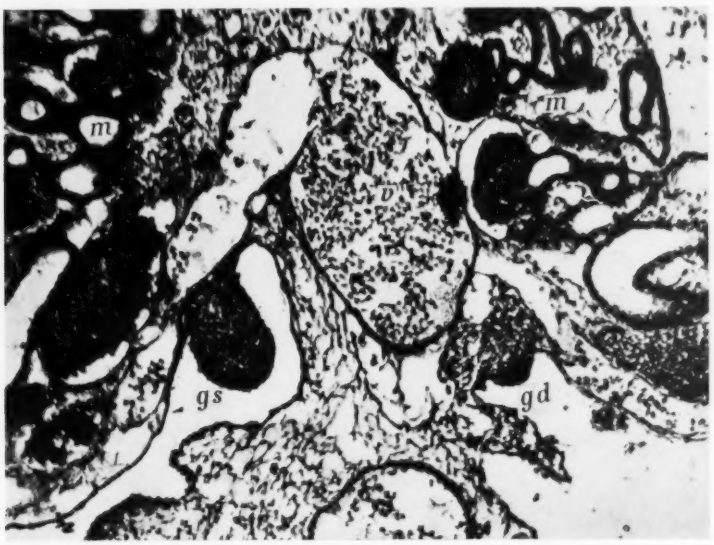

Fig. 6. Dalla sezione trasversale di un embrione trattato con 2 mg di acetato di desossicorticosterone, ucciso all'età di 6 giorni di incubazione (esemplare no. 39); la sezione è stata praticata al livello della massima dimensione delle gonadi. Per la spiegazione delle lettere, vedi alla figura precedente. Si noti la minor grandezza delle gonadi, in confronto all'embrione coetaneo di controllo. Ingrandimento 130 ×.

capace di provocare effetti rilevanti sull'abbozzo delle gonadi, e ha il vantaggio, su quella di 2 mg, di causare una mortalità molto minore.

I risultati raggiunti in questa serie di osservazioni sono raccolti nelle annesse Tabelle IV e V.

TABELLA IV.

Embrioni di pollo di età diverse, normali o ormonizzati. Valori riguardanti la gonade sinistra.

No. d'ordine degli embrioni	Trattamento	Lunghezza della gonade in mm	Volume della cortex	Volume della medulla	Volume complessivo della gonade	Volume percentuale della medulla
Embrioni dell'età di 4 giorni e mezzo di incubazione						
24	Controllo	1,90	—	—	—	—
30	1 mg di ormone	1,66	—	—	—	—
Embrioni dell'età di 5 giorni di incubazione						
25	Controllo	1,71	393,5	772,0	1.165,5	66,2 %
21	1 mg di ormone	1,55	263,0	325,5	588,5	55,3 %
Embrioni dell'età di 5 giorni e mezzo di incubazione						
34	Controllo	1,58	622,5	1.742,0	2.364,5	73,6 %
37	1 mg di ormone	1,40	373,5	519,5	893,0	58,1 %

TABELLA V.

Embrioni di pollo di età diverse, normali o ormonizzati. Valori riguardanti la gonade destra.

No. d'ordine degli embrioni	Trattamento	Lunghezza della gonade in mm	Volume della cortex	Volume della medulla	Volume complessivo della gonade	Volume percentuale della medulla
Embrioni dell'età di 4 giorni e mezzo di incubazione						
24	Controllo	1,58	—	—	—	—
30	1 mg di ormone	1,18	—	—	—	—
Embrioni dell'età di 5 giorni di incubazione						
25	Controllo	1,59	186,5	602,0	788,5	76,3 %
21	1 mg di ormone	1,03	54,0	149,5	203,5	73,4 %
Embrioni dell'età di 5 giorni e mezzo di incubazione						
34	Controllo	1,45	329,5	1.350,5	1.680,0	80,3 %
37	1 mg di ormone	1,10	111,5	331,0	442,5	74,8 %

Come appare dalle Tabelle, per gli embrioni di 4 giorni e mezzo di età non ho potuto calcolare i consueti valori volumetrici delle gonadi, perchè esse in questo stadio di sviluppo, specialmente dopo il trattamento ormonico, non mostrano ancora confini sufficientemente precisi, e soprattutto le loro porzioni midollari si continuano a molti livelli in maniera indefinita con gli abbozzi del tessuto interrenale. Confrontando le gonadi dell'embrione di controllo con quelle dell'embrione ormonizzato, si rileva tuttavia ben chiaramente che già in questo stadio iniziale il volume della medulla delle gonadi è notevolmente ridotto in conseguenza del trattamento con desossicorticosterone: ciò risulta docu-

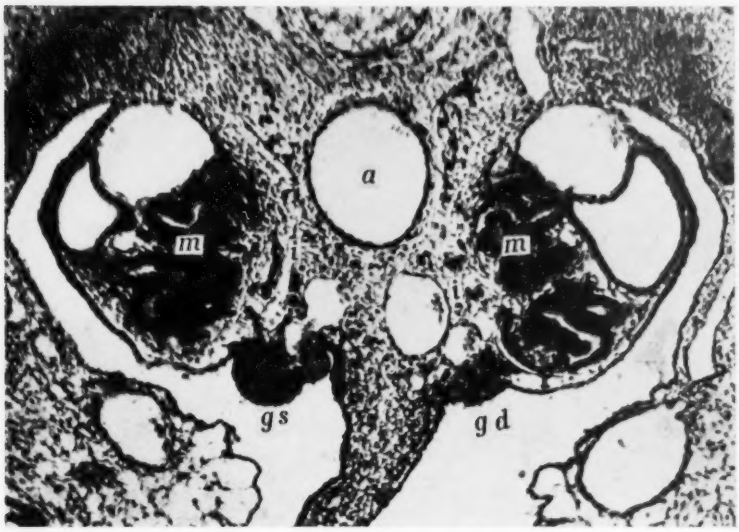

Fig. 7. Dalla sezione trasversale di un embrione normale di controllo, ucciso all'età di 4 giorni e mezzo di incubazione (esemplare no. 24); la sezione è stata praticata al livello della massima dimensione delle gonadi. *gd* gonade destra; *gs* gonade sinistra; *i* tessuto interrenale; *m* mesonefro; *a* aorta. A sinistra è evidente la diretta connessione fra il tessuto interrenale e il tessuto midollare della gonade; a destra tali connessioni sono interrotte, nella fetta considerata, dalla presenza di un vaso sanguigno. Ingrandimento 130 ×.

mentato in modo assai evidente dalle fig. 7 e 8, in cui sono fotografate le sezioni trasversali dell'embrione di controllo e di quello ormonizzato, a un livello in cui le rispettive gonadi mostrano la massima estensione. In entrambi gli embrioni gli abbozzi interrenali sono bene sviluppati; ma nell'embrione ormonizzato è molto scarsa la quantità di tessuto interrenale che, migrando al di sotto della porzione corticale, si trasforma in tessuto midollare delle gonadi.

Per gli embrioni del suddetto stadio di sviluppo, ho misurato soltanto la lunghezza delle gonadi, che è nettamente maggiore negli esemplari di controllo. E' opportuno rilevare che in questa precoce fase embriogenetica la lunghezza normale delle gonadi è maggiore che negli stadi successivi: mano a mano che gli abbozzi delle gonadi si sviluppano e precisano i propri confini, diminuisce infatti la loro estensione longitudinale, nonostante si accresca il loro volume.

Per gli altri embrioni, dell'età di 5 giorni o 5 giorni e mezzo di incubazione, ho potuto agevolmente calcolare, con il metodo descritto, tutti i soliti valori delle dimensioni delle gonadi. I risultati ottenuti non necessitano di un commento troppo lungo, perchè essi, malgrado il numero ristretto degli esemplari esaminati, confermano pienamente quanto abbiamo già descritto per gli embrioni di 6 giorni di età, e dimostrano in maniera molto chiara che gli effetti dell'acetato di desossicorticosterone vengono gradualmente raggiunti durante le varie fasi dello sviluppo dell'abbozzo delle gonadi.

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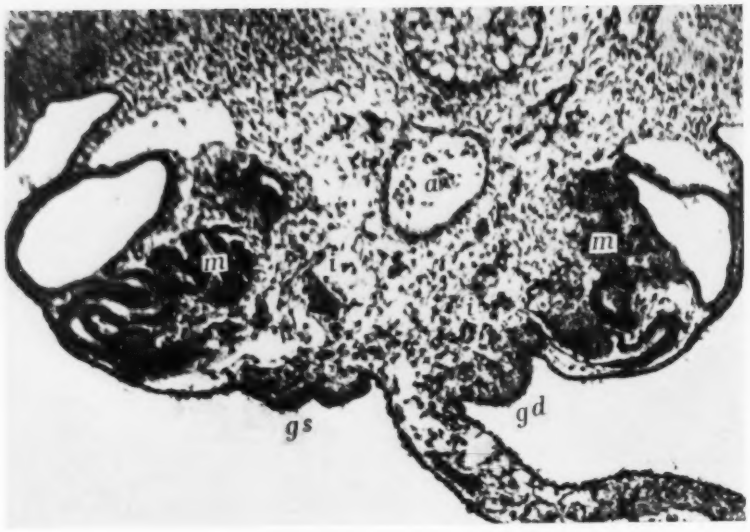

Fig. 8. Dalla sezione trasversale di un embrione trattato con 1 mg di acetato di desossicorticosterone, ucciso all'età di 4 giorni e mezzo di incubazione (esemplare no. 30); la sezione è stata praticata al livello della massima dimensione delle gonadi. Per la spiegazione delle lettere, vedi alla figura precedente. Si noti la minor grandezza delle gonadi in confronto all'embrione coetaneo di controllo, e soprattutto la minor quantità di tessuto midollare proveniente dagli abbozzi interrenali. Ingrandimento 130 ×.

La lunghezza delle gonadi appare costantemente diminuita dal trattamento ormonico, rispetto agli esemplari di controllo, e, come negli embrioni esaminati all'età di 6 giorni di incubazione, tale diminuzione di lunghezza è più notevole per la gonade destra che per la sinistra. Lo stesso può ripetersi anche nei riguardi dei volumi complessivi delle gonadi, che difatti raggiungono sempre valori assai più bassi negli embrioni ormonizzati che in quelli normali di controllo della stessa età; anche in questo caso, la riduzione di volume è soprattutto notevole per la gonade destra. In buon accordo con quanto abbiamo rilevato per gli esemplari uccisi all'età di 6 giorni di incubazione, tale diminuzione di volume è dovuta soprattutto (specialmente nella gonade sinistra) ad una riduzione di grandezza della parte midollare della gonade; la porzione corticale subisce però una diminuzione di volume assai più intensa nella gonade destra che nella sinistra. In conseguenza di tutto ciò, il volume relativo della porzione midollare di ogni gonade, messo in rapporto con il rispettivo volume complessivo, appare sempre più basso negli embrioni ormonizzati che nei coetanei embrioni normali di controllo, però con scarti più ampi nella gonade sinistra che in quella destra di ciascun embrione.

Dai dati della Tabella VI viene inoltre dimostrato che le differenze relative di lunghezza e di volume fra le gonadi destra e sinistra di ciascun embrione, in ognuno degli stadi esaminati, appaiono costantemente più notevoli dopo il

trattamento ormonico che in condizioni normali di sviluppo; questa accresciuta diversità di grandezza consiste soprattutto in un aumento della differenza fra i volumi delle porzioni corticali di destra e di sinistra, perchè il trattamento con acetato di desossicorticosterone accentua molto quella peculiare scarsità di tessuto corticale, che caratterizza, già in condizioni normali, la gonade destra in confronto alla gonade sinistra. Anche da questo punto di vista, gli abbozzi delle gonadi reagiscono dunque all'ormone della corteccia surrenale, fin dagli stadi di sviluppo più iniziali, nella medesima maniera che ho descritta per gli embrioni di 6 giorni di età.

TABELLA VI.

Embrioni di pollo di età diverse, normali o ormonizzati. Rapporti fra le dimensioni delle gonadi destra e sinistra di ciascun embrione.

No. d'ordine degli embrioni	Trattamento	Rapporto fra le lunghezze delle gonadi	Rapporto fra i volumi delle gonadi	Rapporto fra i volumi della cortex	Rapporto fra i volumi della medulla
Embrioni dell'età di 4 giorni e mezzo di incubazione					
24	Controllo	0,83	—	—	—
30	1 mg di ormone	0,71	—	—	—
Embrioni dell'età di 5 giorni di incubazione					
25	Controllo	0,92	0,67	0,47	0,77
21	1 mg di ormone	0,66	0,34	0,20	0,45
Embrioni dell'età di 5 giorni e mezzo di incubazione					
34	Controllo	0,91	0,71	0,52	0,77
37	1 mg di ormone	0,78	0,49	0,29	0,63

Si può concludere che l'acetato di desossicorticosterone inibisce fortemente l'accrescimento del tessuto midollare, e meno fortemente quello della porzione corticale, fin dagli stadi più precoci dello sviluppo delle gonadi. Le riduzioni di volume, che ho notato esaminando le gonadi all'età di 6 giorni di incubazione, non sono dunque — come si sarebbe potuto sospettare — la conseguenza di un arresto di sviluppo verificatosi ad un dato momento dell'organogenesi, ma sono invece provocate da un accrescimento che si dimostra rallentato fino dall'inizio.

DISCUSSIONE DELLE OSSERVAZIONI.

Dai risultati ottenuti appare chiaro che l'acetato di desossicorticosterone ha, sulle gonadi dell'embrione di pollo, la stessa azione medullo-inibitrice da me descritta precedentemente nei girini delle rane; la principale caratteristica degli abbozzi delle gonadi, negli embrioni sottoposti al trattamento sperimentale, è infatti la presenza di un quantitativo troppo scarso di tessuto midollare. Se

riflettiamo che la medulla delle gonadi deriva dagli abbozzi del tessuto interrenale, i risultati ottenuti possono esprimersi dicendo che il trattamento con desossicorticosterone ostacola, in misura crescente con l'aumentare delle dosi, la migrazione delle cellule dagli abbozzi interrenali al territorio della medulla delle gonadi.

Allo stato attuale delle nostre conoscenze, non è possibile dare una sicura interpretazione di questo effetto ormonico, che dobbiamo perciò limitarci a constatare. Sono tentato di ripetere però, anche in questo caso, quanto ebbi a rilevare nel 1944, descrivendo per la prima volta, sui girini delle rane, l'azione medullo-inibitrice dell'ormone della corteccia surrenale. Ostacolando la normale formazione del tessuto midollare delle gonadi, il desossicorticosterone favorisce, in certo senso, una più estesa partecipazione delle cellule dei primitivi abbozzi interrenali alla genesi del tessuto interrenale definitivo, o tessuto della corteccia surrenale; si può così supporre che l'ormone della corteccia surrenale favorisca, nella vita embrionale, lo sviluppo di quello stesso organo che è predestinato a secernerlo nell'adulto. Non diversamente l'estradiolo od il testosterone, stimolando rispettivamente l'accrescimento della porzione corticale o del tessuto midollare delle gonadi, agevolano, durante il periodo embrionale, il differenziamento di quei medesimi organi (ovaie o testicoli) che saranno deputati all'elaborazione di questi stessi ormoni nella vita adulta.

Come abbiamo rilevato, il desossicorticosterone esplica però, accanto alla suddetta azione medullo-inibitrice, anche una meno intensa azione cortico-inibitrice sull'abbozzo delle gonadi: le gonadi degli embrioni di pollo sottoposti al trattamento mostrano infatti in generale anche una deficienza, più limitata, nel volume del tessuto corticale. Come l'azione medullo-inibitrice, anche l'azione cortico- inibitrice appare tanto più intensa quanto più alta è la dose di ormone adoperata. Con basse dosi (0,5 mg), nella gonade sinistra, il volume della porzione corticale non mostra una diminuzione, mentre invece è già diminuito, di circa il 26 %, il volume della porzione midollare.

Possiamo chiederci se ambedue gli effetti rilevati siano una conseguenza diretta del desossicorticosterone, o se invece soltanto l'azione medullo-inibitrice sia un effetto ormonico immediato, e l'azione cortico-inibitrice una conseguenza secondaria del minor volume raggiunto dal tessuto midollare. Considerando l'aspetto stesso degli abbozzi delle gonadi nel pollo, rilevabile dall'esame delle sezioni trasversali, si potrebbe infatti supporre che, quando il tessuto midollare è molto scarso, la cortex si sviluppi con minore intensità semplicemente perchè scarseggia la superficie sulla quale essa normalmente si distende; o si potrebbe comunque supporre l'esistenza di una diretta correlazione fra sviluppo della medulla e accrescimento della cortex nella gonade. Quanto sappiamo sull' antagonismo fra i tessuti corticale e midollare delle gonadi, di cui il primo, come dicemmo, è un territorio potenzialmente ovarico e il secondo potenzialmente testicolare, ci induce tuttavia a ritenere più proba-

bile che un primitivo rallentamento dello sviluppo midollare dovrebbe di per sè avere come conseguenza un più elevato accrescimento della cortex; siamo perciò orientati a ritenere che sia l'azione medullo-inibitrice, quanto la meno intensa azione cortico-inibitrice, siano provocate direttamente dal desossicorticosterone.

Nelle mie prime ricerche sui girini di rana avevo visto solamente l'attività medullo-inibitrice dell'ormone della corteccia surrenale. Ricerche in corso, i cui risultati definitivi verranno presto pubblicati, mi hanno invece più recentemente dimostrato che pure nelle gonadi larvali degli Anfibi il desossicorticosterone, oltre a inibire fortemente lo sviluppo del tessuto midollare, esplica spesso anche una più blanda azione ostacolante l'accrescimento della regione corticale, che si manifesta dapprima con una moltiplicazione meno intensa degli ovogoni e successivamente con un ritardo nella comparsa degli ovociti di I ordine. Posso pertanto affermare l'esistenza di un parallelismo molto esatto fra le azioni dell'acetato di desossicorticosterone sulle gonadi dei girini degli Anfibi e sulle gonadi dell'embrione degli Uccelli.

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Le osservazioni presenti sono state effettuate su gonadi di pollo che non avevano raggiunto l'età del differenziamento sessuale. Esse dimostrano perciò semplicemente che il trattamento con desossicorticosterone, inibendo con intensità diversa lo sviluppo delle porzioni corticale e midollare, fa sì che si organizzino abbozzi di gonadi in cui la proporzione volumetrica fra questi due territori è spostata in favore della cortex, cioè della parte potenzialmente ovarica. Ciò non permette, evidentemente, di affermare che queste gonadi così modificate sian destinate a divenire ovaie nei successivi stadi di sviluppo, indipendentemente dalla costituzione genetica sessuale degli embrioni, e che pertanto l'acetato di desossicorticosterone abbia nel pollo, come in generale negli Anfibi, un vero e proprio effetto femminizzante sull'abbozzo delle gonadi. Se tuttavia le condizioni rilevate all'età di 6 giorni di incubazione dovessero mantenersi immutate oppure accentuarsi nello sviluppo embrionale successivo, è assai probabile che in tutti gli esemplari ormonizzati si assisterebbe a un differenziamento femminile degli abbozzi delle gonadi. Se viceversa negli stadi successivi l'inibizione della cortex dovesse finalmente far risentire il proprio effetto in modo più notevole che l'inibizione midollare, ci si potrebbe attendere uno sviluppo atrofico delle ovaie, oppure addirittura una tardiva mascolinizzazione di esse [1]. Non è neppure da escludere una terza possibilità, e cioè che il trattamento precoce con l'ormone della corteccia surrenale non abbia alcun

[1] Nelle citate mie recenti ricerche, non ancora pubblicate, ho rilevato che, nei girini delle rane, talune dosi di desossicorticosterone mostrano proprio quest'ultimo effetto sullo sviluppo delle gonadi. In un periodo iniziale vengono infatti inibiti, come di consueto, più fortemente lo sviluppo del tessuto midollare e meno fortemente lo sviluppo della cortex, ove si formano nidi di ovogoni. In una fase successiva, però, manca del tutto lo sviluppo degli ovociti nella cortex; gli ovogoni migrano allora nel tessuto midollare, trasformandovisi in spermatogoni, onde la cortex regredisce totalmente. Così le giovani ovaie si trasformano in testicoli.

effetto sulla definitiva proporzione dei sessi negli embrioni di pollo, e che semplicemente si ottengano, in definitiva, ovaie e testicoli meno voluminosi del normale.

Sarà dunque necessaria una successiva serie di ricerche, che, continuando quelle attualmente riferite, possa permettere di precisare le definitive conseguenze del trattamento precoce con l'ormone della corteccia surrenale, su gonadi di embrioni di pollo di età più progredita. Un primo tentativo di questo genere è fallito, perchè, iniettando — con la consueta tecnica — 1 mg di acetato di desossicorticosterone in 10 uova poste ad incubare da 48 ore e aprendo poi le uova all'età di 12 giorni di incubazione, ho rilevato che nessun embrione era sopravvissuto. Sembra pertanto che la metodica sperimentale dovrà perfezionarsi, per ottenere una più lunga e abbondante sopravvivenza degli embrioni, senza però abbassare l'efficacia del trattamento ormonico. In ogni modo, i risultati fin qui raggiunti mi sono parsi degni di essere resi noti, perchè essi ci consentono di caratterizzare chiaramente le azioni esercitate dall'ormone steroide esaminato. Abbiamo visto infatti che *il desossicorticosterone inibisce lo sviluppo di tutto quanto l'abbozzo delle gonadi, ma soprattutto della sua porzione midollare*. Lo si può dunque considerare una sostanza *a prevalente azione medullo-inibitrice ed a più scarsa azione cortico-inibitrice*. Qualunque siano gli effetti terminali del trattamento con desossicorticosterone, essi non sembrano perciò paragonabili, per meccanismo di azione, a quelli del testosterone o degli ormoni estrogeni.

Merita ancora qualche commento l'effetto differente del trattamento ormonico sulle due gonadi, destra e sinistra, di ciascun embrione. Come si è visto, esso fa sì che risulti nettamente accentuata la consueta scarsità relativa di volume dell'abbozzo della gonade destra, e soprattutto fa sì che in questa gonade ipoplasica sia più elevata che di norma la scarsità del tessuto corticale. Sicuramente questa maggiore azione inibitrice dell'acetato di desossicorticosterone deve esser messa in rapporto con le ben note peculiari condizioni di sviluppo della gonade destra nell'embrione degli Uccelli. Fin da precoci stadi, quest'ultima si accresce, normalmente, con intensità minore che la gonade sinistra, e soprattutto se ne atrofizza la porzione corticale. Osservazioni del WITSCHI (1935), da me estese e confermate (VANNINI 1945 a), mostrano chiaramente che nell'embrione di pollo gli elementi germinali, inizialmente ripartiti in ugual numero nelle regioni genitali dei due lati, a partire dall'età di circa 4 giorni di incubazione divengono nettamente meno numerosi a destra che a sinistra.

Come è generalmente risaputo, tale precoce asimmetria dell'apparato genitale è destinata successivamente a conservarsi e accentuarsi negli esemplari femminili, che all'età adulta sono provvisti della sola ovaia sinistra, mentre a destra mostrano semplicemente un rudimento di gonade, formato quasi soltanto di tessuto midollare. Negli esemplari maschili, invece, la stessa asimmetria si attenua fortemente e scompare quasi del tutto, onde gli adulti presentano

ambedue i testicoli perfettamente conformati e funzionanti. L'asimmetria giovanile degli abbozzi delle gonadi appare dunque legata soprattutto ad una molto scarsa capacità di sviluppo della regione corticale destra, e ad una meno intensa scarsità di accrescimento del tessuto midollare dello stesso lato; il trattamento con acetato di desossicorticosterone accentua queste peculiarità della gonade destra.

Si noti che anche in tutti gli esperimenti precedenti (WOLFF, WILLIER, DANTSCHAKOFF, VAN OORDT e RINKEL), effettuati con ormoni androgeni od estrogeni, è stata rilevata una diversa reattività delle gonadi destra e sinistra dell'embrione degli Uccelli. Così gli estrogeni (estrone, estradiolo), negli esemplari geneticamente maschili, trasformano in ovaia o in ovotestis soltanto la gonade sinistra, mentre l'abbozzo della gonade destra conserva un aspetto testicolare o si atrofizza.

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Nelle ricerche sui girini degli Anfibi (VANNINI 1944, 1945 b, 1946, 1947 a) ho ritenuto di poter paragonare l'attività medullo-inibitrice del desossicorticosterone con quella della cortessina inibitrice, che — come mostrano gli esperimenti di parabiosi effettuati dal WITSCHI — viene secreta dalla porzione corticale delle ovaie larvali ed inibisce lo sviluppo del tessuto midollare. Questo confronto sarebbe prematuro per gli Uccelli, perchè finora non è stato dimostrato che anche l'ovaie di questi Vertebrati producano, durante la vita embrionale, una cortessina inibitrice. Esperimenti recenti del WOLFF (1947 b) hanno infatti dimostrato che innestando ovaie embrionali di pollo in altri embrioni molto giovani, non ancora sessualmente differenziati ma di sesso genetico maschile, la gonade sinistra dell'ospite si evolve parzialmente in direzione femminile; sembra però che quest'azione femminizzante dell'innesto non sia dovuta a una sostanza medullo-inibitrice, simile alla cortessina inibitrice ammessa dal WITSCHI per gli Anfibi, ma che essa sia invece attribuibile a una precoce produzione di ormone follicolare ovarico, che stimola direttamente l'accrescimento e la differenziazione di un tessuto corticale sulla gonade del maschio.

Resta perciò da chiederci se anche normalmente, nello sviluppo dell'embrione degli Uccelli, gli ormoni steroidi della corteccia surrenale — del tipo del desossicorticosterone — possano svolgere qualche influenza, se non proprio sul differenziamento sessuale, per lo meno sull'organizzazione dell'abbozzo delle gonadi. Indubbiamente all'età di 2 giorni di incubazione, epoca in cui ho iniettato nell'uovo il desossicorticosterone, questo ormone non viene ancora secreto dal tessuto interrenale (che nell'embrione di pollo comincia a svilupparsi, dalla parete peritoneale, circa all'età di 3 giorni e mezzo), e non è ancora normalmente presente nel sangue o nei tessuti dell'embrione. Perciò le azioni medullo-inibitrici, da me ottenute sperimentalmente in fasi assai precoci, probabilmente sono del tutto artificiali e non trovano riscontro nelle condizioni

fisiologiche che si verificano nell'ontogenesi normale di embrioni della stessa età.

Si deve tuttavia rilevare che condizioni ben diverse si notano all'età di 5 giorni e mezzo e di 6 giorni di incubazione, quando normalmente si interrompe la continuità fra gli abbozzi interrenali e la medulla delle gonadi, onde si arresta la migrazione di cellule dai primi alla seconda. In questi stadi di sviluppo, il tessuto interrenale ha ormai un aspetto che può permetterci di considerarlo all'inizio di una funzionalità, non certo intensa, ma sufficiente per esplicare forse qualche effetto; molte sue cellule tendono infatti ad ordinarsi in forma di cordoni, e fra di esse inizia la penetrazione degli elementi cromaffini (Brezzi 1940). Si può pertanto prospettare, in via di ipotesi, che negli embrioni al sesto giorno di età la rilevata rottura delle connessioni fra abbozzi interrenali e medulla delle gonadi sia provocata, o per lo meno favorita, da un'incipiente secrezione di desossicorticosterone (o di altri ormoni dello stesso tipo) da parte del tessuto interrenale. In questo caso l'azione medullo-inibitrice sperimentalmente ottenuta, e dipendente da un rallentamento precoce della migrazione di elementi cellulari dagli abbozzi interrenali alla regione midollare delle gonadi, consisterebbe in un anticipo e in un'accentuazione di quello stesso effetto ormonico che normalmente è destinato a verificarsi un po'più tardi.

A complemento delle presenti osservazioni devo aggiungere che, negli embrioni esaminati, il trattamento con desossicorticosterone in nessun caso ha anticipato il differenziamento del tessuto interrenale, nè ha favorito un suo sviluppo più abbondante del normale.

RIASSUNTO.

Le presenti ricerche sono state effettuate con l'intento di accertare se anche negli embrioni di pollo — come nei girini degli Anfibi — un ormone sintetico della corteccia surrenale (l'acetato di desossicorticosterone) influisca sullo sviluppo dell'abbozzo delle gonadi.

Nell'albume di uova di pollo, incubate da 48 ore, sono state iniettate quantità diverse di una soluzione oleosa di acetato di desossicorticosterone (Percorten Ciba), e le gonadi degli embrioni sono state esaminate istologicamente all'età di 6 giorni di incubazione, oppure, in un numero minore di casi, in età più giovanili. Valutazioni quantitative hanno messo in evidenza che le gonadi degli embrioni ormonizzati sono sensibilmente più piccole di quelle degli embrioni normali della stessa età, e che questa ipoplasia è dovuta soprattutto ad uno scarso sviluppo del tessuto midollare; assai meno cospicua è la riduzione di volume della parte corticale degli abbozzi delle gonadi.

Questi effetti ormonici hanno una differente intensità sugli abbozzi delle gonadi destra e sinistra di ciascun embrione, onde si accentua, negli embrioni

ormonizzati, la normale condizione di ipoplasia relativa della gonade destra e lo stato di atrofia della sua porzione corticale.

In perfetta analogia con quanto accade nei girini degli Anfibi (VANNINI 1944, 1947 c), anche negli embrioni di pollo il desossicorticosterone esplica dunque, durante lo sviluppo degli abbozzi delle gonadi, una forte azione medullo-inibitrice ed un'azione cortico-inibitrice meno intensa. Ne risultano abbozzi delle gonadi nei quali il rapporto fra i volumi delle porzioni corticale e midollare è spostato, in confronto agli embrioni normali di controllo, a favore della porzione corticale. Ulteriori ricerche dovranno precisare se tale alterata composizione degli abbozzi delle gonadi si ripercuota — come avviene nei girini degli Anfibi — sull'ulteriore differenziamento sessuale. E' possibile tuttavia, fin d'ora, tentare di mettere in rapporto l'attività medullo-inibitrice del desossicorticosterone con l'origine embriologica del tessuto midollare delle gonadi dagli abbozzi del tessuto interrenale (VANNINI 1943); si può pure prospettare, in via di ipotesi, che l'ormone della corteccia surrenale intervenga anche normalmente sullo sviluppo dell'abbozzo delle gonadi, arrestando, al sesto giorno di età, l'ulteriore migrazione di elementi cellulari dagli abbozzi interrenali alla regione midollare delle gonadi.

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SUMMARY.

The present researches have been made to ascertain if in chick embryos—as in anuran larvae—a synthetic cortico-adrenal hormone (desoxycorticosterone acetate) has any influence on the development of gonadal blastema.

Various quantities of desoxycorticosterone acetate oily solution (Percorten Ciba) have been injected in the albumen of fowl eggs, at the age of two days' incubation, and the embryos' gonads were histologically observed at the age of six days' incubation, or, in some cases, in younger stages. Quantitative valuations demonstrated that the gonads of treated embryos are sensibly smaller than those of normal embryos, and that such hypoplasia is due, above all, to scarce development of the medullary tissue; much less conspicuous is the reduction of volume of the gonadal cortex.

The effects produced by desoxycorticosterone have different intensity on the blastema of the right and left gonad in the same embryo; therefore normal conditions of relative hypoplasia of the right gonad, and atrophy of its cortical portion, are more evident in hormonised embryos.

Then desoxycorticosterone carries out, during development of the gonadal blastema in chick embryos, a strong medulla-inhibiting action and a less vigorous cortex-inhibiting one, exactly as it happens in anuran larvae (VANNINI 1944, 1947 c). As a consequence, the normal proportion between volume of the cortex and that of the medulla, changes, in comparison with control embryos,

in advantage of the cortical component. Further researches will point out if such modifications in the gonadal blastema have any effect on the successive sex-differentiation, as it happens in anuran larvae. However it is possible, for the present, to suppose some relation between the medulla-inhibiting action of desoxycorticosterone and the embryological origin of the gonad's medulla from the interrenal blastema (VANNINI 1943); we are likewise led to suppose, as a hypothesis, that the cortico-adrenal hormone also acts in the normal development of the gonadal blastema, inhibiting, at the age of six days, the further migration of cells from the interrenal blastema to the medullary territory of the gonads.

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DIE GAUMENLÜCKEN DER VÖGEL

VON

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(Mit 16 Abbildungen im Text.)

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I. EINLEITUNG.

Die Gaumenlücken der Reptilien sind wiederholt untersucht und auf die der Amphibien zurückgeführt worden. Zusammenfassende Darstellungen jüngeren Datums finden sich bei BOAS (1914), LAKJER (1927) und VERSLUYS (1936). Von einigen verstreuten Bemerkungen abgesehen hat man sich mit dem Lückensystem des Vogelgaumens m. W. bisher noch nicht beschäftigt, wenngleich seine knöchernen Elemente schon lange genauestens studiert waren. Die Lücken des Vogelgaumens behandelte man meist kurz im Anhang an die Reptilien. Hier wirkte sich der systematische Begriff der *„Sauropsida"* sehr nachteilig aus, der in Einem zusammenfaßt, was der Entwicklungsrichtung nach weit auseinanderstrebt. Mindestens im Schädelbau können die Vögel den Reptilien als ebensogut geschlossene Einheit gegenübergestellt werden wie die Säuger; ähnliches dürfte für andere Organsysteme gelten. Es ist beabsichtigt durch einen Vergleich mit dem Reptilgaumen die Abwandlung des Lückenmusters festzustellen und die Homologiefrage der einzelnen Spalten zu klären. Andernorts und zu späterem Zeitpunkt wird der funktionelle Sinn der Umbildungsvorgänge erörtert werden. Die Begriffe Gaumen und Munddach verwenden wir im Sinne LAKJERS (1927, S. 59). Während der Drucklegung dieser Arbeit erschien der erste Teil der Untersuchungen von MCDOWELL (1948) über den knöchernen Gaumen der Vögel. Es war deshalb leider nicht mehr möglich, diese außerordentlich wertvolle Arbeit hier zu verwerten.

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II. DIE LÜCKEN DES MUNDDACHES UND IHRE BEZIEHUNGEN ZU DEN ARTEN DER SCHÄDELKINETIK.

Wenn, wie von VERSLUYS u. a. wiederholt dargelegt wurde, das Muster der Gaumenlücken aus der Kinetik des Schädels verstanden werden kann, dann ist klar, daß bei verschiedenen Grundformen der Kinetik auch verschiedene Lückenmuster gefunden werden müssen. Es wurde ein branchio-, splanchno- und neurokinetischer Typus unterschieden (HOFER 1945 b, S. 364) von denen nur die beiden letzten für uns in Betracht kommen. Bei der Splanchnokinetik wird nur der Kieferbogen, eventuell auch das ihm angeschlossene Hyomandibulare, aktiv seitlich geschwenkt, während das Neurokranium in sich starr bis zur Schädelspitze durchzieht. Knochenelemente des Kieferbogens und des Schädelkieles bilden gemeinsam das Munddach (Abb. 1). Der Kiemenkorb behält die Branchiokinetik bei, die wir für primitiv ansprechen wollen, indem er nur dehnende und kontrahierende Bewegungen ausführt. Bei der Neurokinetik kann der Rostralteil des Neurokranium (Maxillarsegment, VERSLUYS) gegen das Occipitalsegment bewegt werden. Der Kieferbogen, der direkt oder indirekt mit beiden Teilen verbunden sein kann, wird besondere Beanspruchungen erfahren, da er sowohl mit dem fixierten als auch mit dem beweglichen Teil in Kontakt steht. Auch er kann noch laterale Schwenkungen ausführen. Beide kinetischen Zustände können auch akinetische Formen aus sich hervorgehen lassen. Die Splanchnokinetik finden wir in reiner Form bei den *Holostei, Teleostei* u. a., die Neurokinetik bei den *Crossopterygii* und Tetrapoden. Bei beiden sind die Spezialisationszustände der Neurokinetik wesentlich verschieden.[1]

Die erste mechanische Bedingung der Splanchnokinetik ist durch das starr bis zur Rostralspitze des Schädels durchlaufende Neurokranium gegeben, an

[1] Soweit bisher zu überblicken ist, stellen die unterschiedenen kinetischen Typen schon mehr oder weniger scharf geprägte Spezialisationen dar, die durch keine querverlaufende Spezialisationsreihe verbunden werden können. Phylogenetische Tiefenverbindungen müssen wohl angenommen werden. Auf solche näher einzugehen verbietet der Rahmen der Arbeit, doch sei vor allem auf PFANNENSTIEL (1932) verwiesen. Die dort beschriebene Pleurokinetik ist vielleicht ein außerordentlich interessanter Sonderfall der aus der Neurokinetik zu verstehen ist, ähnlich der Streptostylie.

dem der Kieferbogen lateral beweglich befestigt ist. Daraus geht klar hervor, daß niemals eine Gaumendurchbrechung auftreten kann, die das Munddach quer unterteilt. Hingegen müssen Spalten auftreten, die den Gaumenanteil des Kieferbogens von dem des Schädelkieles trennen. Die zweite Bedingung ist, daß nirgends starre Verbindungen zwischen Neurokranium und Kieferbogen auftreten, weil sonst jegliche Bewegung im splanchnokinetischen Sinne gesperrt würde. Das typische splanchnokinetische Munddach (Abb. 1) zeigt also immer paarige Längsspalten, niemals einen unpaaren Medianspalt oder Querspalten, weil der Schädelkiel persistiert. Deshalb wirkt auch das splanchnokinetische Munddach nicht als Einheit, wie das neurokinetische, bei dem der ganze Gaumen rostral bewegt wird und beim Biß zur Wirkung kommt. Auch beim splanchnokinetischen Gaumen finden wir neben den Spalten, die den neurokranialen Anteil des Gaumens (Praemaxillare, Vomeres und Parasphenoid) vom splanchnischen (Palatinum, Pterygoidea primordialer und dermaler Herkunft) trennen, Längsspalten, die das Maxillare von Palatinum und Ectopterygoid scheiden, caudal offen bleibend.[1] Diese lateralen Spalten entsprechen den Adductorlücken (Vgl. S. 243) des Tetrapodenschädels, die erst sekundär geöffnet wurden, als das Quadratojugale nicht mehr entwickelt wurde.

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Die mechanische Bedingung der Neurokinetik ist die querverlaufende Unterteilung des Neurokranium, das in zwei mehr oder weniger bewegliche Abschnitte (Segmente) getrennt wird. Daraus ergibt sich, daß im Gaumen immer Spalten vorhanden sein müssen, die in ihrer Lage u n g e f ä h r dem das Neurokranium trennenden Spalt entsprechen und die Aufgabe haben in der Median — Sagittalebene verlaufende Bewegungen des rostralen Segmentes zu ermöglichen. Solche Spalten können als Querspalten aufgefaßt werden, auch dann, wenn sie nicht senkrecht auf die Medianebene verlaufen. Durch sie wird der Gaumen ebenfalls in einen bewegten und einen fixierten Abschnitt geteilt, wenn das auch ursprünglich nicht immer äußerlich erkennbar sein muß. Im noch wenig durchgebildeten Zustande der Neurokinetik werden vielleicht noch splanchnokinetische Eigenbewegungen des Kieferbogens möglich sein. Jedoch leuchtet ein, daß bei dorso-ventralen Bewegungen des Maxillarsegmentes eine laterale Nachgiebigkeit des Kieferbogens die Einheitlichkeit und Wirkung des Bisses stört. Daher versteht man, daß der neurokinetische Schädel zum Unterschied vom splanchnokinetischen die neurokranialen Anteile des Maxillarsegmentes mit den splanchnokranialen fest zusammenschließt. Darum sind Dermalknochen der Spitze des Neurokranium (Praemaxillare) mit solchen des Kieferbogens (Maxillare und z. T. Palatinum) zum kraftvollen Biß fest zusammengefügt. Im Bereiche des Mundwinkels, wo der stark beanspruchende, zermalmende Biß ausgeführt wird, vereinigt das Transversum (Ectopterygoid)

[1] Die Ausdrücke Neuro- und Splanchnokranium verwenden wir hier im Sinne Marinellis (1936).

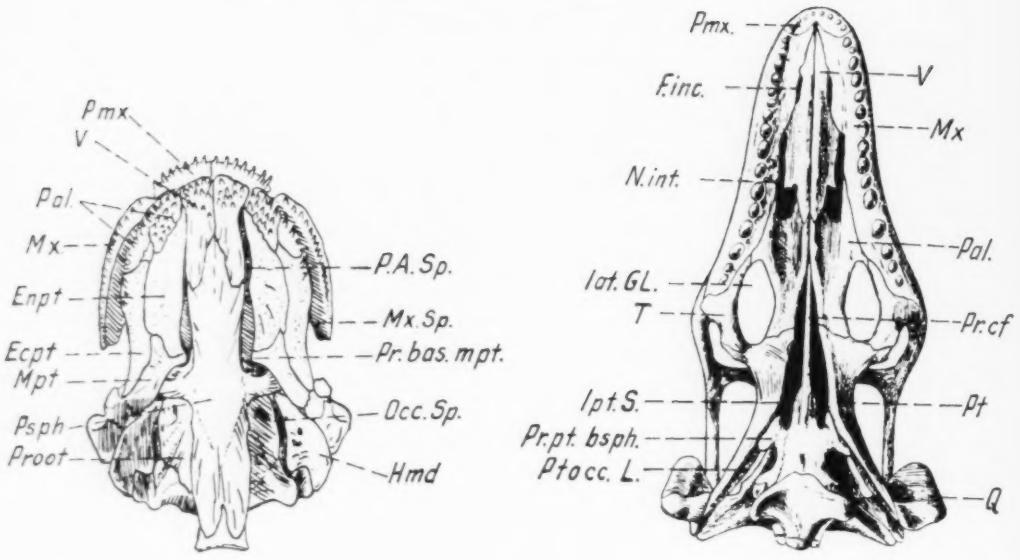

Abb. 1 A—B. Splanchnokinetischer Fischgaumen (Holosteertypus) und neurokinetischer Reptilgaumen (Lacertiliertypus). A: *Amia calva*, umgezeichnet nach GOODRICH (1930). B: *Tupinambis teguixin* nach VERSLUYS (1936). *Hmd* Hyomandibulare; *Ecpt* Ectopterygoid; *Enpt* Entopterygoid; *F.inc.* Foramen incisivum; *Ipt.S.* Interpterygoidalspalt; *lat.GL.* laterale Gaumenlücke; *Mpt* Metapterygoid; *Mx* Maxillare; *Mx.Sp.* Maxillarspalt; *N.int.* Nares internae; *Occ.Sp.* Occipitalspalt; *Pal.* Palatium; *P.A.Sp.* Parachsialspalt; *Pmx* Praemaxillare; *Pr.bas.mpt.* Processus basalis metapterygoidei; *Pr.cf* Processus cultriformis; *Proot* Prooticum; *Pr.pt.bsph.* Processus pterygoideus basisphenoidei; *Psph* Parasphenoid; *Pt* Pterygoid; *Ptocc.L.* Pteroccipitallücke; *Q* Quadratum; *T* Transversum; *V* Vomer.

die medialen Gaumenteile des Kieferbogens (Palatinum und Pterygoid) mit dem Maxillare. Das Parasphenoid wird zum Processus cultriformis und zieht sich bei kinetischen Formen von der Bildung des rostralen Abschnittes des Munddaches völlig zurück (Abb. 1 B). Der Typus der Neurokinetik wäre bei Stegokephalen und älteren Reptilien zu finden; vgl. die ausgezeichneten Untersuchungen von PFANNENSTIEL (1932). Die von VERSLUYS unterschiedene Meta-, Meso- und Amphikinetik sind neurokinetische Sonderfälle.

Von den Reptilien übernahmen die Vögel die Neurokinetik, die sich hier in nicht immer deutlich geschiedenen Sondertypen findet. Wir müssen also beim Vogelgaumen ein Lückenmuster erwarten, das aus der Neurokinetik zu verstehen ist.

Der Unterschied zwischen der Mesokinetik der Reptilien und dem ähnlichen Typus der Vögel besteht darin, daß bei ersteren die Beugungszone in der überwiegenden Mehrzahl der Fälle zwischen Frontale und Parietale verläuft, während sie bei letzteren immer vor den Augen liegt und mit der interethmoidalen Fissura cranio-facialis in Zusammenhang steht. Aus diesem Typus leitet sich die Rhynchokinetik (HOFER 1945 a) ab, die in verschiedenen

Stämmen der Vögel zur Ausbildung kommt und verhältnismäßig selten ist. Bei ihr liegt die Beugungszone noch weiter rostral, vor dem Etmoidalskelett, so daß die Fissura cranio — facialis verschwindet und in manchen Fällen das Praemaxillare von den Nasalia und Maxillaria gelockert werden kann. Den letzteren Zustand findet man bei den *Limicolae, Crypturi* und Ratiten verschieden deutlich ausgeprägt. MOLLER (1930, S. 658) nannte diesen Typus prokinetisch, während ich ihn rhynchokinetisch nannte. Es scheint mir richtiger den MOLLERschen Terminus auf alle Vögel anzuwenden, weil bei ihnen die Beugungszone praeorbital, also vor der Beugungszone des mesokinetischen Reptiltypus liegt. Von Rhynchokinetik sollte nur dann gesprochen werden, wenn die Biegung im Schnabel, also praeethmoidal erfolgt. In Fortsetzung der von VERSLUYS angewandten Terminologie scheint mir ein solches Vorgehen geboten zu sein um zum Ausdruck zu bringen, daß die Beugungszone nach rostral verlegt wird: Aus der Metakinetik entwickelt sich — wenigstens nach den bisher gültigen Vorstellungen —, über die vermittelnde Amphikinetik die reine Mesokinetik und aus dieser wieder die Prokinetik, die bei den Vögeln in einigen Fällen die Rhynchokinetik hervorgehen läßt.

Der die Entstehung der Prokinetik erhellende Zusammenhang scheint in der Augenvergrößerung zu liegen, die schon bei den *Pseudosuchia* begann und bei *Archaeornis* ein erhebliches Ausmaß erreichte. Diese und die damit im Zusammenhang stehende Vergrößerung des Gehirns schloß eine fronto-parietale Beugung im Schädeldach aus. Jede Hebung des Oberkiefers erzwingt aber eine Biegung im Schädeldach, sofern dessen Drehpunkt nicht mit dem des Quadratum zusammenfällt; diese Biegung wird sich vorteilhaft als Knickung äußeren, für die nur mehr das praeorbitale Gebiet in Frage kommt. So könnte man die Ausbildung des prokinetischen Zustandes durch die Volumszunahme der Augen und des Gehirnes erklären und annehmen daß er schon bei den reptilhaften Vogelvorfahren entwickelt wurde. Für die Entstehung der Rhynchokinetik aus der Prokinetik fehlen mir noch die eine befriedigende Erklärung ergebenden Zusammanhänge. Ihr Auftreten im System (Ratiten, *Crypturi, Limicolae* u. a.) und die Verschiedenheit ihrer speziellen Differenzierungszustände lassen vermuten, daß sie nicht nur an verschiedenen Stellen des Vogelstammes entstand, sondern auch ihre Entwicklung durch unterschiedliche Zusammenhänge zu erklären sein wird.

Der hier angeschnittene Problemkreis bedarf noch weiterer Durcharbeitung, einerseits an dem seit den Tagen der VERSLUYSschen Untersuchungen erheblich angewachsenen fossilen Material, anderseits auch an rezenten Formen, denn was inzwischen über die Kinetik des Tetrapodenschädels bekannt wurde, läßt vermuten, daß viel mannigfachere Verhältnisse innerhalb der einzelnen größeren Formenkreise vorliegen als VERSLUYS ursprünglich annehmen konnte. Immer deutlicher zeigt sich, daß das Problem der Kinetik eine viel durch-

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greifendere Bedeutung für die Morphologie des Kopfes hat, als man anfänglich anzunehmen geneigt war, was besonders für die Kopfmuskulatur gilt.

III. DIE LÜCKEN DES REPTIL- UND VOGELGAUMENS.

1. DIE LÜCKEN DES REPTILGAUMENS.

Soweit von Reptilien gehandelt wird, braucht nur der kinetische Gaumen berücksichtigt zu werden.[1] Die den Gaumen in einen maxillaren und occipitalen Anteil trennenden Spalten sind verschieden groß und reichen verschieden weit nach vorne. Sie trennen die Pterygoidea, Palatina und teilweise auch die Vomeres und scheiden caudal die Schädelbasis von den Elementen des Maxillarsegmentes (Abb. 1). Diese medialen Spalten werden von LAKJER (1927) „Mittelspalten" genannt. Sie werden durch das Basipterygoidgelenk überbrückt und dadurch in zwei ungefähr hintereinander liegende Spalten getrennt, die in der Literatur verschieden benannt wurden. Den rostralen Teil wollen wir mit VERSLUYS (1912) Interpterygoidalspalt nennen; er wird nicht immer vollständig durch den Processus cultriformis parasphenoidei in einen rechten und linken Teil geschieden. Er macht die tiefergreifenden gestaltlichen Veränderungen durch als das ihm caudal folgende Spaltenpaar, die Pteroccipitallücken (BOAS 1914), und wird von Pterygoid und Palatinum umschlossen, kann aber rostral zwischen die Vomeres eindringen. Die Pteroccipitallücken liegen hinter dem Basipterygoidgelenk und werden lateral vom Pterygoid, medial vom Basioccipitale und Basisphenoid begrenzt und bleiben caudal offen. Als Teile des Spaltensystems, welches Maxillarsegment und Occipitalanteil des Schädels scheidet, müssen sich Interpterygoidalspalten und Pteroccipitallücken bei kinetischen Schädeln immer finden. Bei akinetischen Schädeln, die die Beweglichkeit erst jüngst verloren haben (*Plesiosaurus, Sphenodon* u. a.), sind sie ebenfalls noch vorhanden. Bei stark kinetischen Schädeln (*Ophidia*) ist der Interpterygoidalspalt am stärksten ausgeprägt und schwindet mit dem Auftreten akinetischer Zustände am frühesten.

Die lateral und rostral der Mittelspalten liegenden Gaumenlücken finden sich im Gaumenabschnitt des Maxillarsegmentes. LAKJER (1927, S. 63) faßt sie als Unterteilungen eines einzigen Seitenspaltes auf und unterscheidet demnach „Vorder-, Mittel- und Hinterseitenspalt". Wir wollen die ältere Terminologie zu ihrer Kennzeichnung wählen, da es unangängig erscheint diese Durchbrechungen serial gleichzusetzen. LAKJER kam zu dieser Auffassung durch seine wenig glückliche Unterscheidung von „Innen- und Außengaumen-

[1] Wir gehen auf die Verhältnisse der Reptilien nur kurz ein, soweit sie für den Vogelgaumen von Wichtigkeit zu sein scheinen. Umfangreichere Bearbeitungen des Reptil- und Amphibiengaumens finden sich bei BOAS (1914), LAKJER (1927), VERSLUYS (1927, 1936) und STADTMÜLLER (1936).

bogen". Die vordersten Öffnungen sind die primären Choanen über deren sehr wechselnde Verhältnisse bei den Reptilien LAKJER (1927) und BUSCH (1898) berichteten. Je nach ihrer Ausdehnung werden die Choanen verschieden knöchern umfaßt. Lateral und rostral sind es immer Elemente des Dermalkiefers (Maxillare), medial und caudal Knochen der neurokranialen Schädelbasis (Praemaxillare und Vomeres) und das Palatinum.

Auf die Choanen folgt die sehr verschieden große laterale Munddachlücke (BOAS 1914). Sie liegt in dem Gebiet wo Maxillare, Palatinum, Transversum und Pterygoid zusammentreffen; diese Knochen können in verschiedenem Ausmaße an der Umrahmung dieser Lücke beteiligt sein. Von den randständigen Gaumenlücken ist sie die einzige, die membranös verschlossen ist. Die Membran wird nach LAKJER (l. c. S. 63) von „mehreren Nervenzweigen des N. infraorbitalis trigemini und N. palatinus facialis" durchstoßen. BOAS (1914, S. 260) findet am Schädel von *Pareiasaurus* eine laterale Gaumenlücke, ebenso bei den Pelycosauriern *Edaphosaurus* und *Dimetrodon*. Bei rezenten Reptilien ist sie allgemein vorhanden (Abb. 1). Nun meint BOAS unter Hinweis auf die durch diese Lücke durchtretenden Nerven, daß sie „als abgetrennter Teil der Mediopalatinlücke (i. e. Interpterygoidalspalt unserer Terminologie) aufgefaßt werden" müsse (l. c. S. 264), denn bei den Anuren gehe der entsprechende Nerv durch ebendiese Lücke. Eine laterale Gaumenlücke fehlt den Anuren. Das Nervenverhalten ist für BOAS das entscheidende Argument, eine solche Abspaltung der lateralen Gaumenlücke von dem Interpterygoidalspalt zu vermuten, obwohl er sich der Schwierigkeiten dieser Annahme bewußt ist, die darin besteht, daß keine Spur eines ehemaligen Zusammenhanges der beiden Öffnungen zu finden ist. LAKJER kommt zur feststellung einer Homologie zwischen der lateralen Gaumenlücke der Reptilien und einer ähnlichen Öffnung bei *Polypterus* auf Grund eines Nervendurchtrittes — eine hier nicht zu erörternde Frage —, doch läßt er das von BOAS aufgeworfene Problem offen (l. c. S. 224, 230, 239). VERSLUYS (1936, S. 737) spricht die sicherlich berechtigte Vermutung aus, daß dit laterale Gaumenlücke auch selbständig aus dem erwähnten Nervenloch entstanden sein könnte. Dieser Ansicht wollen wir uns anschließen und halten die laterale Gaumenlücke für eine Erweiterung eines Nervenloches, die vielleicht im Zusammenhang mit der Tendenz den Schädel graziler zu gestalten, verständlich ist. Dabei kann es zu einer Verschmelzung der lateralen Gaumenlücke mit der ihr caudal folgenden Adductorlücke so lange nicht kommen, als das Transversum als mediale Abstützung des Maxillare nötig ist. Daher findet man die Lücke nur klein bei den alten, massivschädeligen Formen, augenfällig aber bei den jüngeren, höherspezialisierten, grazilschädeligen. Ihr Fehlen bei manchen Fossilschädeln kann damit erklärt werden, daß der Nachweis eines Nervenforamens bei solchem Material nicht immer möglich sein dürfte.

Die größte, von den Fischen übernommene Öffnung im Munddach der Rep-

tilien ist die „Untere Schläfenöffnung", die dem Durchtritt der Adductoren dient und des halb hier Adductorlücke genannt sei. Sie liegt immer lateral des Palatoquadratum, rostral des Quadratum und medial des unteren Jochbogens, falls ein solcher vorhanden ist. Bei den *Ophidia* und *Lacertilia* (Abb. 1), denen ein unterer Jochbogen fehlt, ist sie lateral offen.

Diese Lückenmuster im Gaumen der Reptilien wurde von den Vögeln übernommen und wahrscheinlich schon an der Wurzel dieses Stammes beträchtlich verändert.

2. DIE LÜCKEN DES VOGELGAUMENS.

a. *Interpterygoidalspalt und Pteroccipitallücke.*

Wir betrachten die Öffnungen des Munddaches der Vögel an *Otis tarda* (Abb. 2), einer als recht ursprünglich anzusehenden Form, die weder einer auf frühem phylogenetischen Zustand einsetzenden Reliktspezialisation verfiel, noch später eine durchgreifende Spezialisierung erlebte — beides ließe sie aberrant erscheinen — und deshalb geeignet ist als typischer Vogelgaumen den morphologischen Ausgangspunkt der folgenden Betrachtungen zu bilden.

Beim Vogelgaumen, der immer kinetisch bleibt — über *Casuarius* vgl. S. 238 — sind Interpterygoidalspalt und Pteroccipitallücke immer vorhanden, doch können sie durch Verlust des Basipterygoidgelenkes verschmelzen und einen einheitlichen, caudal offenen Gaumenmittelspalt bilden. Dieser Vorgang, der sich bei manchen Familien ontogenetisch leicht verfolgen läßt (*Accipitres, Otides, Balaeniceps* u. a.; vgl. Abb. 2), kann funktionell verstanden werden (Böhm 1930, Starck 1940, Hofer 1945 a); dabei handelt es sich darum dem Pterygoid eine erweiterte laterale Bewegungsmöglichkeit zu verschaffen, wie sie besonders bei stark kinetischen Schädeln erforderlich sein kann. Der Interpterygoidalspalt, bzw. der einheitliche Gaumenmittelspalt trennt im ursprünglichen Zustand auch die Palatina und kann schlitzartig von caudal in den bei den Vögeln im erwachsenen Zustand einheitlichen Vomer eindringen, die beiden Vomerschenkel voneinander scheidend. Dieser rostrale Teil des Interpterygoidalspaltes ist eigentlich keine Gaumenlücke mehr, denn er wird dorsal durch das Rostrum sphenoidale verschlossen, das bei den Vögeln kräftig ausgebildet weiter nach vorne reicht als bei den Reptilien, wo es als Processus cultriformis vielfach sogar im Interpterygoidalspalt selbst frei endigt. Diese stärkere Ausbildung des Rostrum sphenoidale hängt mit dem bei den Vögeln entwickelten prokinetischen Typus zusammen. Bei diesem können die im Verhältnis zur Beugungslinie weit caudal liegenden Basipterygoidgelenke als Gaumenstütze nicht mehr genügen. Daraus läßt sich verstehen, daß die Palatina in der Längsrichtung verschieblich gegen das Keilbeinrostrum angelegt werden, welches durch das Septum interorbitale und die Pars perpendicularis mesethmoidei von dorsal gestützt wird. Der die Palatina im ursprünglichen Zu-

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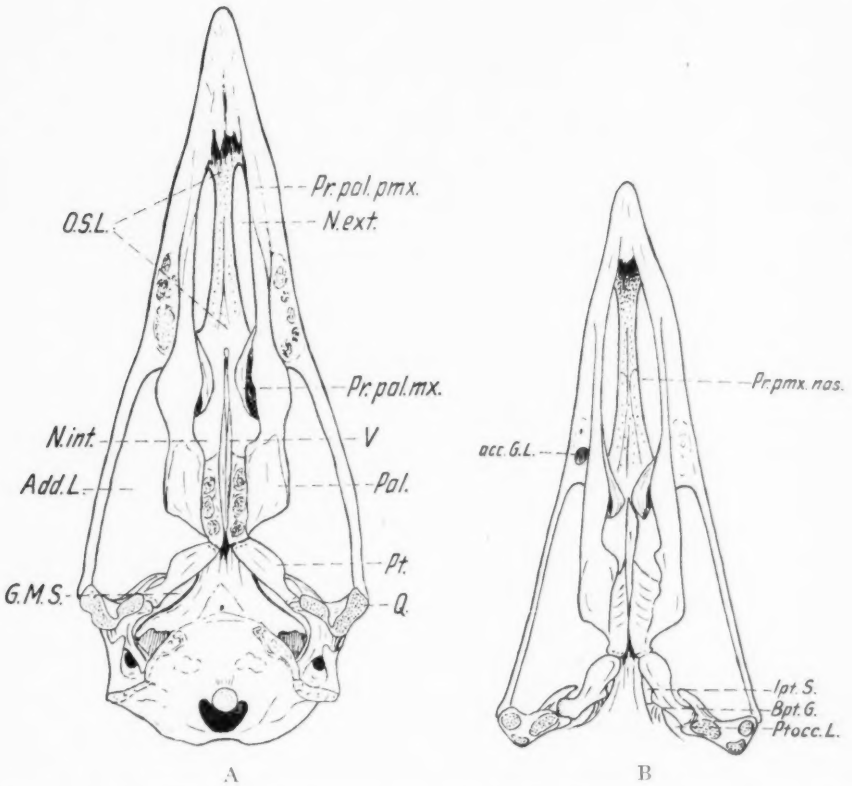

Abb. 2 A—B. Primitiver Vogelgaumen von *Otis tarda*. Beachte die verschiedene Ausbildung der accessorischen Gaumenlücken. A: Erwachsenes Tier, ohne Basipterygoidgelenke (Orig.). B: Jungtier mit funktionierenden Basipterygoidgelenken (Orig.). *acc.G.L.* Accessorische Gaumenlücken; *Add.L.* Adductorlücke; *Bpt.G.* Basipterygoidgelenk; *G.M.S.* Gaumenmittelspalt, hervorgegangen aus Verschmelzung von *Ipt.S.* und *Ptocc.L.*; *N.ext.* äußere Nasenöffnungen in der Gaumendurchsicht; *O.S.L.* Oberschnabellücke; *Pr.pal.pmx.* Processus palatinus praemaxillaris; *Pr.pal.mx.* Processus palatinus maxillae; *Pr.pmx.nas.* Processus praemaxillaris nasalis. Die übrigen Bezeichnungen wie bei Abb 1.

stande trennende Spalt ist also, wie der Vergleich mit dem Reptilgaumen ergibt, als vorderster Teil des Interpterygoidalspaltes aufzufassen, wenn er auch bei den Vögeln durch das Keilbeinrostrum verschlossen werden kann. Ich habe früher (1945 a) diesen die Palatina, eventuell auch den Vomer teilweise trennenden Teil des Interpterygoidalspaltes Diastema genannt. Man kann diese Bezeichnung aufrecht erhalten, denn sie kennzeichnet einen Teil des Interpterygoidalspaltes, der sein eigenes Geschick hat und dadurch besonders hervortritt. So rücken bei verschiedenen Vogelstämmen die Caudalenden der Palatina entlang des ventralen Umfanges des Rostrum sphenoidale aneinander, so daß sie in wechselseitigen medialen Kontakt kommen, bindegewebig straff

verbunden werden, ja sogar verschmelzen können (Sympalatinie), wodurch das Diastema schwindet. So wie die Anlagerung der Caudalenden der Palatina an das Rostrum sphenoidale funktionell verständlich ist (HOFER 1945 a, S. 107 ff.), erkennen wir auch diesen Spezialisationsschritt als aus demselben Prinzip erfolgend, nämlich eine möglichst sichere aber auch rostral liegende Führung des Gaumenskelettes am Neuralschädel zu erreichen. Durch die mediale Vereinigung der Palatina wird erreicht, daß diese sich wechselseitig stützen, wodurch wieder die Verbindung mit dem Rostrum sphenoidale entlastet und damit auch freier beweglich wird, aber nichts an Sicherheit der Führung einbüßt. Diesen sympalatinen Zustand finden wir daher auch bei stark kinetischen und bedeutenden Beanspruchungen ausgesezten Schädeln.[1] Ja es kann soweit kommen, daß sich auch die Pterygoidköpfe wechselseitig berühren, natürlich ohne zu verschmelzen, weil sonst jede Bewegung gesperrt würde. Dadurch kommt es zu einer weiteren Einengung des Interpterygoidalspaltes von rostral (*Ciconiae* u. a.). In selteneren Fällen (*Lari*) kann es zu einer Abtrennung des Diastemas vom Interpterygoidalspalt dadurch kommen, daß sich nur die Caudalenden der Palatina medial vereinigen, rostral dieser Stelle aber wieder auseinanderweichen. Gerade dieser Fall zeigt deutlich den funktionellen Zusammanhang solcher Veränderungen, denn sie setzen dort ein, wo eine besondere Gefährdung des Gaumenskelettes besteht, im Gebiete des Pterygo-Palatingelenkes. Durch die mediale Verbindung der Palatinenden, auch wenn es noch keine Verschmelzung ist, wird die Gefahr von Luxationen vermieden. Schon das Bisherige läßt erkennen, daß der vorderste Teil des Interpterygoidalspaltes, das Diastema, Einflüssen unterliegt, die funktionell unter dem Gesichtspunkt der Sicherung und Führung des Gaumenskelettes am Keilbeinrostrum verständlich sind. Auch die folgenden Fälle lassen sich unter diesem Gesichtspunkt bewerten. Kann es einerseits zur Reduktion des Diastemas kommen, so ist andererseits, wenn auch seltener, das Gegenteil zu beobachten: Das Diastema wird erhalten, manchmal sogar etwas verbreitert. Einerseits sind nun zur Sicherung und Führung des Gaumenskelettes am Keilbeinrostrum neue Vorkehrungen nötig, anderseits tritt damit ein neues Bild der Gaumenlücken auf, das zwar Ähnlichkeit mit dem von Formen mit Basipterygoidgelenk hat, morphologisch ihm aber nicht vergleichbar ist.

Bei den *Galli* und *Anseres* findet sich ein wohlausgebildetes Gelenk zwischen dem etwas verstärkten Caput pterygoidei und dem Rostrum sphenoidale (Abb. 3), das keinesfalls dem Basipterygoidgelenk zu homologisieren ist, dann

[1] Eine Ausnahme dieser Regel bilden die *Striges*, die zwar hoch kinetische, aber nicht außerordentlich belastete Kieferapparate besitzen. Sehr wahrscheinlich steht die Entwicklung der Sympalatinie bei manchen Gattungen der Eulen im Zusammenhang mit der außerordentlichen Pneumatisierung des Schädels, die auch auf den Kieferapparat übergreift und hier besonders den Vomer befällt. Dadurch verschmelzen die Palatina mit dem Vomer, so daß schließlich ein rein sympalatiner Zustand resultiert (*Tyto alba*).

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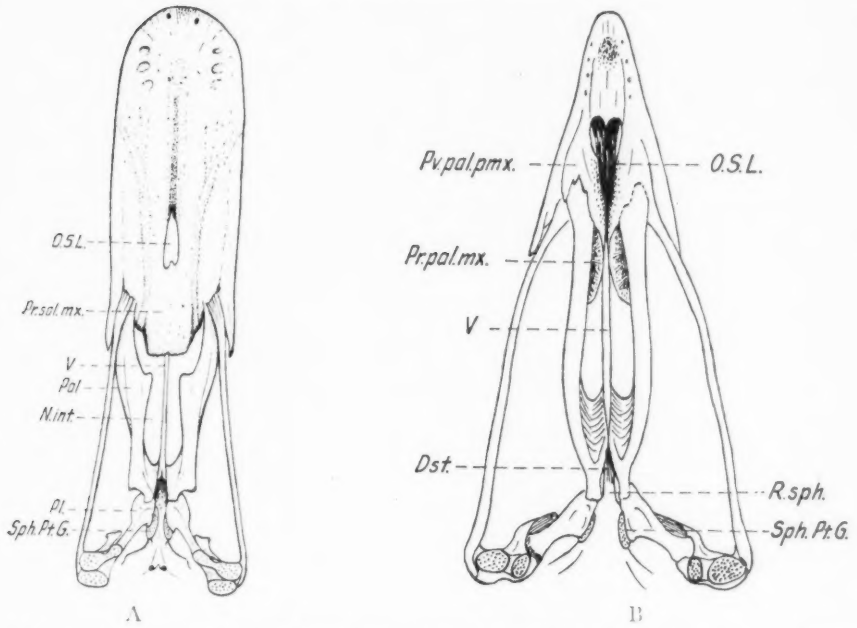

Abb. 3 A—B. Accessorische Spheno-Pterygoidgelenke und bleibendes Diastema. A: *Cygnus olor*, Typus der Anseres (Orig.). B: *Crax sp.*, Typus der Galli (Orig.). *Dst.* Diastema; *R.sph.* Rostrum sphenoidale; *Sph.Pt.G.* Spheno-Pterygoidgelenk.

müßte es weiter caudal liegen, sondern eine Neubildung darstellt.[1] Es ist ein accessorisches Spheno-Pterygoidgelenk, das als Gleitlager des Gaumenskelettes funktioniert und darin dem Basipterygoidgelenk analog ist. Durch das Spheno-Pterygoidgelenk wird eine seitliche, festere und sichere Führung des Gaumenskelettes erreicht, was gleichzeitig bedingt, daß die Capita pterygoidea und die mit ihnen gelenkig verbundenen Caudalenden der Palatina in ihrer ursprünglichen Lage seitlich am Rostrum sphenoidale festgehalten werden, so daß eine mediade Verlagerung der Gaumenspangen nicht möglich ist, allerdings auch nicht mehr nötig wird, denn die Sicherung der Führung am Keilbeinrostrum, deren die Gaumenknochen bedürfen und die sie eben durch ihre mediale Verlagerung zu erreichen trachten, ist schon durch das accessorische Spheno-Pterygoidgelenk erworben. In solchen Fällen bleibt das Diastema bestehen, ja

[1] Ein ähnliches Gelenk findet sich auch bei den *Anhimae*. Stresemann (1924—34, S. 708) hält es für ein sekundäres Basipterygoidgelenk, Gadow (1893, S. 152) und Beddard (1868, S. 455) halten es für ein echtes; vgl. dazu auch Parker (1863), Garrod (1876), Mitchell (1895), Beddard (1886, 1894). Beddard setzt es dem der *Anseres* gleich und diagnostiziert beide Bildungen als Basipterygoidgelenke; letzteres ist sicher falsch. Solange keine ontogenetischen Stufen untersucht sind ist eine Entscheidung mit Sicherheit nicht möglich, doch möchte ich mich wegen der caudaleren Lage der Gelenke bei den *Anhimae* eher der Ansicht Gadows anschließen.

es kann die Palatina sogar völlig trennen (*Tetrao*). Rostral wird das Diastema durch den Vomer geschlossen, in den es verschieden tief eindringen kann.

Ein ähnliches Bild finden wir bei *Bubo bubo* (Abb. 4), doch kam es hier noch nicht zur Bildung eines accessorischen Spheno-Pterygoidgelenkes. Vielleicht ist letzteres durch die noch vorhandenen und voll funktionierenden Basipterygoidgelenke zu erklären, da schon diese eine, wenn auch nicht immer ausreichende Sicherung des Pterygo-Palatinegelenkes bilden. Wir finden bei *Bubo* an der Stelle wo sich die Köpfe der Pterygoidea gegen das Keilbeinrostrum legen, an diesem eine deutliche ventrale Intumescenz (Abb. 4, *Int.*), die auf stärkerer auf diese Stelle beschränkte Pneumatisierung des Knochens beruht. Diese Intumescenz zwischen den Pterygoidköpfen und den Caudalenden der Palatina bewirkt, daß diese getrennt bleiben und das Diastema erhalten bleibt; dieses wird rostral durch den Vomer und seine beiden scharf nach lateral strebenden Crura abgeschlossen. Zwei Tatsachen kennzeichnen den bei *Bubo* gefundenen Zustand als ursprünglicher als den der *Galli* und *Anseres:* Erstens das Vorhandensein voll funktionierender Basipterygoidgelenke, zweitens das Fehlen einer Gelenkdifferenzierung im Bereiche der Instumescenz.[1]

Vergleicht man die besprochenen Gaumenlücken bei Hühnern und Gänsen mit denen solcher Formen, die noch ein Basipterygoidgelenk besitzen, etwa *Otis* juv. (Abb. 2 B), so ist eine entfernte Ähnlichkeit feststellbar, die jedoch keineswegs Homologie bedeutet. Die Lücke, die bei den *Anseres* und *Galli* durch das Pterygoid und Basisphenoid umrahmt wird, umfaßt sowohl die Pteroccipitallücke, als auch den Teil des Interpterygoidalspaltes, der etwa bis in Höhe des Pterygo-Palatingelenkes reicht. Die Gaumenspalte, die bei Gänsen und Hühnern zwischen Pterygoid und Schädelbasis sich findet, stellt demnach ein Verschmelzungsprodukt der Pteroccipitallücke und des caudalen Teiles des Interpterygoidalspaltes dar; der rostrale Teil des letzteren erleidet als Diastema sein besonderes Geschick. Demnach ist die erwähnte Gaumenlücke der Hühner und Gänse zwar der entsprechenden solcher Formen gleichzusetzen, die ein Basipterygoidgelenk verloren haben (*Otis* adult, Abb. 2 A), niemals aber einer

[1] Es wurde schon darauf hingewiesen (S. 218) daß auch bei den *Striges* ein sympalatiner Zustand erworben wird, wodurch das Diastema schwindet. Da mir reicheres, gut bestimmtes Skelettmaterial im Augenblick nicht zur Verfügung steht, konnte der Prozess nicht genauer analysiert werden, doch hat es den Anschein, als sei bei den *Striges* dieser Zustand durch enorme Pneumatisierung des Vomer zu erklären. Damit stellt diese Gruppe einen Sonderfall dar, denn der Sinn der Sympalatinie scheint in möglichst sicherer, aber doch beweglicher Führung der Gaumenspangen am Keilbeinrostrum zu liegen. Eine solche zusätzliche Sicherung hat aber nur dann einen Sinn, wenn der Gaumenapparat starken Belastungen ausgesetzt ist (*Bucerotidae* u. a.), was gerade für die Eulen im besonderen Maße nicht zutrifft und unter diesen wieder am wenigsten für *Tyto alba*, bei der sich der sympalatine Zustand am ausgeprägtesten findet. Wenn man beachtet, daß bei *Tyto* die Pneumatisierung des Schädels außerordentliche Ausmaße erreichte und im besonderen der Vomer so stark pneumatisiert ist, daß er von dorsal betrachtet geradezu aufgelöst erscheint und bedenkt, daß die Pneumatisierung des Knochens am Vogelschädel weitgehend parallel geht mit der Verschmelzung der Knochenindividuen, so scheint es vertretbar, einen Zusammenhang zwischen der Pneumatisierung des Vomer und der Sympalatinie bei *Tyto* anzunehmen.

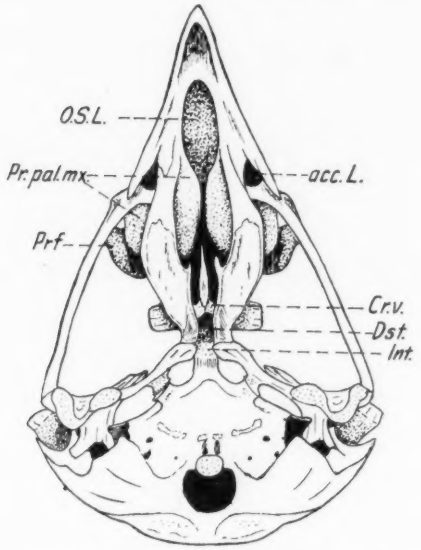

Abb. 4. Accessorische Gaumenlücken, bleibendes Diastema und Intumescenz des Rostrum sphenoidale bei *Bubo bubo* (Orig.). *Cr.v.* Crus vomeris; *Int.* Intumescentia rostri sphenoidalis; *Prf* Praefrontale.

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der Gaumenlücken, von Formen die ein Basipterygoidgelenk besitzen, denn nicht das accessorische Spheno-Pterygoidgelenk scheidet die beiden Spalten, sondern das Basipterygoidgelenk. Diese beiden Gelenke sind aber nicht homologe Bildungen.

Einige Unterschiede in der Umrahmung des Interpterygoidalspaltes bestehen bei den straußenartigen Vögeln, von denen wir nur die rezenten Formen untersuchen können. Das Basipterygoidgelenk ist immer vorhanden und erreicht eine Ausbildung, die für diese Formen für typisch angesehen wurde (HUXLEY 1867, PYCRAFT 1900, 1901,). Bei *Struthio* (Abb. 16) ist der Interpterygoidalspalt klein. Das erklärt sich z. T. daraus, daß die Pterygoidea ihre für die Palaeognathie kennzeichnende Verbindung mit dem Vomer verloren haben und sich wahrscheinlich im Zusammenhang damit nun breiter an das Rostrum sphenoidale anlegen. Bei *Dromaius, Casuarius* und *Rhea* finden sich untereinander weitgehend ähnliche Zustände. Der Interpterygoidalspalt läuft rostral spitz zu, verschieden weit in den Vomer eindringend. Bei *Apteryx* sind die Interpterygoidalspalten nach den Adductorlücken die breitesten Gaumenöffnungen (Abb. 14). Bei allen palaeognathen Gaumen, ausgenommen bei *Struthio,* wird der Interpterygoidalspalt in verschiedenem Ausmaße rostral auch durch den Vomer begrenzt, denn diese Gaumenform ist eben dadurch gekennzeichnet, daß Vomer und Pterygoid in Kontakt bleiben. Diese Umrahmung findet sich auch bei den *Crypturi.* Ob darin allerdings ein prinzipieller

Unterschied gegenüber dem neognathen Gaumen zu erblicken ist, erscheint fraglich.

Vergleicht man Interpterygoidalspalt und Pteroccipitallücke der Reptilien mit denen der Vögel, so fällt die weitgehende Übereinstimmung auf. Die geringfügigen Unterschiede in Lage, Form und Umrahmung treten angesichts des weiten phylogenetischen Abstandes zwischen Reptilien und Vögeln zurück. Einleitend wurde schon bemerkt, daß die beiden medialen Gaumenlücken nur die vom Munddach her sichtbaren Teile jenes Spaltensystems sind, das den neurokinetischen Schädel in ein maxillares und occipitales Segment zerlegt und das seinen funktionellen Sinn eben in den neurokinetischen Bewegungen im Schädel hat, sei es daß diese aktiv, sei es daß sie passiv ausgeführt wurden. Schon VERSLUYS wies nach, daß dieses Spaltensystem den Neuralschädel in verschiedener Höhe zerlegen kann, wonach Unterformen der Neurokinetik unterschieden werden können (vgl. S. 212). Überblickt man diese, so erkennt man, daß von dem inneren Schädelbewegungen bedingenden Spaltensystem nur die Gaumenanteile (Interpterygoidalspalt und Pteroccipitallücke) festgehalten werden, während die den Neuralschädel zerlegenden Spalten bei jedem Typus anders liegen, so daß die Spalten des in der Spezialisationshöhe und vielleicht auch phylogenetisch voraufgehenden Typus veröden können. So wurden beim metakinetischen Schädel die Primordialelemente des Hinterhauptes von den dermalen des Außenpanzers geschieden, beim mesokinetischen Schädel liegen die Trennungslinien zwischen Frontale und Parietale, während die occipitale langsam verödet. Bei der Prokinetik der Vögel liegt der Schädel — Gesichtsspalt fronto-nasal und interethmoidal, während von den beiden vorigen Spaltensystemen keine Spur erkennbar bleibt und bei der Rhynchokinetik trifft den interetmoidalen Spalt dasselbe Schicksal. Im krassen Gegensatz dazu steht das auffällige Beharren der Gaumenteile der sonst bei jedem Typus wechselnden, den Schädel in die gegeneinander beweglichen Teile trennenden Spaltensysteme. Den erklärenden Zusammenhang erblicken wir darin, daß die Bewegung, sofern sie aktiv ausgeführt wird, vom Quadratum und Pterygoid ihren Ausgang nimmt, denn so lange müssen diese beiden Elemente, aber auch die rostral von ihnen liegenden zum funktionellen System gehörigen, beweglich erhalten werden, was eben durch die Interpterygoidalspalten und Pteroccipitallücken geschieht. Wird die Bewegung des Oberkiefers nur mehr passiv ausgelöst, etwa durch kräftige Bisse oder starkes Zustoßen mit dem Schnabel, dann müssen die beiden Knochen so lange beweglich bleiben, als sie und die sie bewegenden Muskeln dazu bestimmt sind, den Impuls abzufedern; auch in letzterem Falle müssen die Interpterygoidalspalten und Pteroccipitallücken erhalten bleiben. Ich vermute daß die Schädelbewegungen der straußenartigen Vögel nach diesem Modus verlaufen.

b. *Innere Nasenöffnungen und ihre Derivate.*

Die praeetmoidale Streckung der Kiefer bei der Bildung des Schnabels hat zu tiefgreifenden Änderungen der Proportionen im Bereiche des Munddaches geführt. Die Umbildung und in manchen Vogelordnungen sehr weitgehende Reduktion des Vomer änderte das Lückenmuster. Läßt ersteres die Länge der inneren Nasenöffnungen verstehen, so erklärt letzteres ihre teilweise oder gänzliche Verschmelzung am Skelettschädel. Wir führen das breite Fenster, das bei sehr vielen Vogelordnungen fast an der Spitze des Oberkiefers beginnt und bis in die Höhe des Vorderrandes der Orbita reicht und von Praemaxillare, Maxillare, Palatinum und dem verschieden großen Rest des Vomer begrenzt wird, auf die Choanendurchbrechung des Reptilgaumens zurück. Die ursprüngliche Trennung der Choanen durch den Vomer wird am Skelettschädel nur mehr im caudalen Abschnitt dieses Fensters angedeutet, wo der Vomer in dieses hineinragt, die beiden Nasen-Rachengänge voneinander scheidend.[1] Wir wollen das unpaare, rostromedian liegende Gaumenfenster Oberschnabellücke nennen, da die Bezeichnung Choane deswegen nicht zutreffend erscheint, weil man damit die Öffnung der Nasen-Rachengänge bezeichnet, die nur einen Teil dieser Lücke einnehmen und von ihr meist häutig, manchmal auch knöchern geschieden sind. Außerdem läßt sich die Ausdehnung der Oberschnabellücke nicht durch das Ausmaß der Choanen erklären, sondern ist ein Derivat der Nares internae der Reptilien und ist in ihrer enormen Ausdehnung für den primitiven Vogelgaumen characteristisch (Abb. 2).

Die Erklärung der Rückbildung der Vomeres, die an der Entstehung der Oberschnabellücke maßgeblich beteiligt ist, ist angesichts des Fehlens vermittelnder fossiler Formen nur durch Vermutungen möglich. Vielleicht ist die praethmoidale Streckung der Kiefer bei etwa gleichzeitiger Reduktion des Geruchsorganes bei den Vögeln und ihren Vorfahren der wichtigste Faktor gewesen. Die Vomeres sind die Elemente des knöchernen Munddaches die bauplanmäßig den ventralen Schutz des Geruchsorganes zu übernehmen haben und damit in ihren Schicksalen an dieses gebunden sein könnten. Es wäre dann zu verstehen, daß mit der Reduktion des Geruchsorganes auch die Vomeres der Rückbildung verfallen. Auch aus den hebenden Kieferbewegungen könnten Zusammenhänge gefunden werden, die die Reduktion der Vomeres verständlich

[1] Ohne eine vollständige Reduktion des Vomer bei manchen Vögeln leugnen zu wollen, sei betont, daß solche Angaben nur mit Sicherheit gemacht werden können, wenn auch mikroskopisch kein knöcherner Vomer nachgewiesen werden kann. Der vielfach skalpellförmige Vomer liegt nämlich an der Ventralkante einer straffen, in der Medianebene liegenden Membran, die von der Rostralkante der Pars perpendicularis mesethmoidei durch die Fissura cranio-facialis an den Hinterrand des knöchernen oder knorpeligen Septum nasi des Oberkiefers zieht; diese Membran gehört zum Bindegewebsskelett der Nase und scheidet die beiden Choanengänge. Nun ist es sehr leicht möglich, daß in dieser Membran, deren ventraler Rahmen eben der messerklingenförmige Vomer ist, Rudimente desselben erhalten bleiben, die bei der Mazeration leicht verloren werden, vor allem dann, wenn ihre Verbindung mit dem Palatinum gelockert ist.

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machen. Ein vollentwickelter Vomer würde beim Vogelgaumen die Palatinfortsätze der Praemaxillaria mit dem Caudalende der Palatina oder den Köpfen der Pterygoidea verbinden. Damit wäre er bei jeder Schnabelhebung Biegungen ausgesetzt, die zu Spannungen führen müßten, die für den ganzen Kieferapparat hinderlich wären und seine Beweglichkeit einschränkten. Diese fallen weg, sowie die Vomeres ihre rostrale Verbindung mit den Praemaxillaria verlieren. Daß diese Vermutungen, mit denen eine Wissenlücke überbrückt werden könnte, nicht voll befriedigen ist klar, doch ist ein anderer Weg solange nicht gangbar, als fossiles Material fehlt, das den Reptilgaumen schrittweise an den der Vögel anzuschließen vermag.

Der beschriebene Zustand der weiten Eröffnung des Schnabelgaumens ist nach der Terminologie von HUXLEY (1867) schizognath, weil die Gaumenfortsätze der Maxillaria durch die Oberschnabellücke geschieden werden. Die Primitivität der Schizognathie, die wohl allgemein anerkannt ist, wird besonders durch die Ontogenie gestützt, indem rein desmognathe Formen bis in späte Jugendstadien hinein eindeutig schizognath sind. Einen Sonderfall dieses für die Vögel primitiven Gaumentypus finden wir bei den *Passeres* (Abb. 5) und *Micropodidae*. Er ist durch eine besondere Form des Vomer kenntlich und bedingt dadurch ein Lückenmuster, das sonst nur bei Formen mit caudal geschlossener Schnabellücke, also bei einem desmognathen Zustand, gefunden wird. Der Vomer ist eine, etwa in der Gaumenebene liegende Platte, die sich caudal durch zwei kräftige Crura mit den Palatina, bzw. Hemipterygoidea verbindet. Die Gaumenfortsätze der Maxillaria sind gestielt und terminal meist deutlich verbreitert. Sie verschmelzen nicht vechselseitig und kommen auch in keinen Kontakt mit dem Vomer. Die Oberschnabellücke wird durch den Vomer und die beiden maxillaren Gaumenfortsätze von den Choanen getrennt, so daß im rostralen Gaumenteil drei Fenster gefunden werden, ähnlich wie bei primitiv desmognathen Formen (manche *Anseres*). Von letzteren ist der Gaumen der *Passeres* und *Micropodidae* dadurch unterschieden, daß die Oberschnabellücke nicht durch ein einheitliches Knochenband, sondern durch drei, in verschiedenen Ebenen liegende, voneinander gesonderte Knochenelemente caudal abgeschlossen und von den Choanen getrennt wird. Sowie eine der Komponenten ganz oder teilweise reduziert wird, kommt ein Lückenmuster heraus, das dem des primitiven Gaumens entspricht, also schizognath ist. Schon das allein zeigt, daß der Gaumen der *Passeres* und *Micropodidae* zu unrecht von HUXLEY zu einem eigenen Typus erhoben wurde („Aegithognathie"); vielmehr ist er der Schizognathie zuzurechnen (u. a. BEDDARD 1898, S. 139 ff.; HOFER 1945 a, S. 147 ff.).[1]

[1] Ob auf die Gestalt des Vomer der *Passeres* wirklich der systematische Wert zu legen ist, den ihr GADOW beimessen will, scheint zweifelhaft. Erstens herrscht innerhalb des Stammes eine bedeutende noch nicht voll zu überblickende Variation darin und zweitens findet man rostral verbreiterte und zweizipfelige Vomeres auch in anderen, mit den *Passeres* zweifellos nicht näher verwandten Vogelgruppen. Gerade die *Micropodidae*

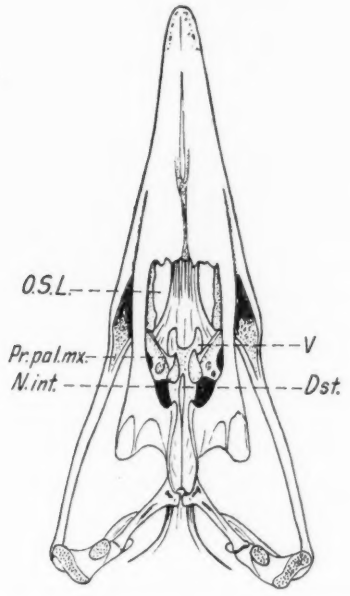

Abb. 5. Caudale, unvollständiger Verschluß der Oberschnabellücke durch Vomer und Processus palatinus maxillaris („Aegithognathie") bei *Corvus scapulatus* (Orig.).

Daß aus der primitiven Schizognathie wiederholt die Desmognathie hervorgeht, ist eine feststehende Erkenntnis. Dieser Vorgang ist auch funktionell als Kieferverstärkung verständlich. Hier interessiert uns nur das Schicksal der Munddachöffnungen, deren Muster bei dieser Umbildung modifiziert wird. Bei zahlreichen Vogelstämmen besteht die Tendenz, die Oberschnabellücke zu schließen, so daß der Spangenaufbau des Oberkiefers, der durch die weiten äußeren Nasenöffnungen und die Oberschnabellücke bedingt ist, durch eine massivere Konstruktion ersetzt wird. Natürlich beschreiten solche Formen diesen Spezialisationsweg nicht, die, den Spangenaufbau weiterspezialisierend, diesen zum Konstruktionsziel erheben (*Laro-Limicolae*). Die zum Verschluß der Oberschnabellücke führende Entwicklungstendenz läßt verschiedene Spezialisationsstufen erkennen, die von PARKER (1876, 1878) und im Anschluß an ihn von GADOW (1891, S. 990) zusammengestellt wurden.

Die Umformungen der Oberschnabellücke bei Erwerbung der Desmognathie sollen im folgenden nur an einigen Spezialisationsstufen untersucht werden, wobei wir mit den *Anhimae* und *Anseres* beginnen. Bei diesen findet man For-

können als Beispiel hierfür gelten. M. E. ist auf die Form des Vomer der *Passeres* nicht mehr Wert zu legen als auf die Messerklingenform desselben, die ebenfalls auf bestimmte Verwandtschaftsgruppen beschränkt sein kann (*Laro-Limicolae*), aber auch bei anderen Familien auftritt. Vermutlich ist die Gestalt des Vomer auch aus der Anatomie des Geruchsorganes zu erklären, doch sind mir darüber noch keine Untersuchungen bekannt.

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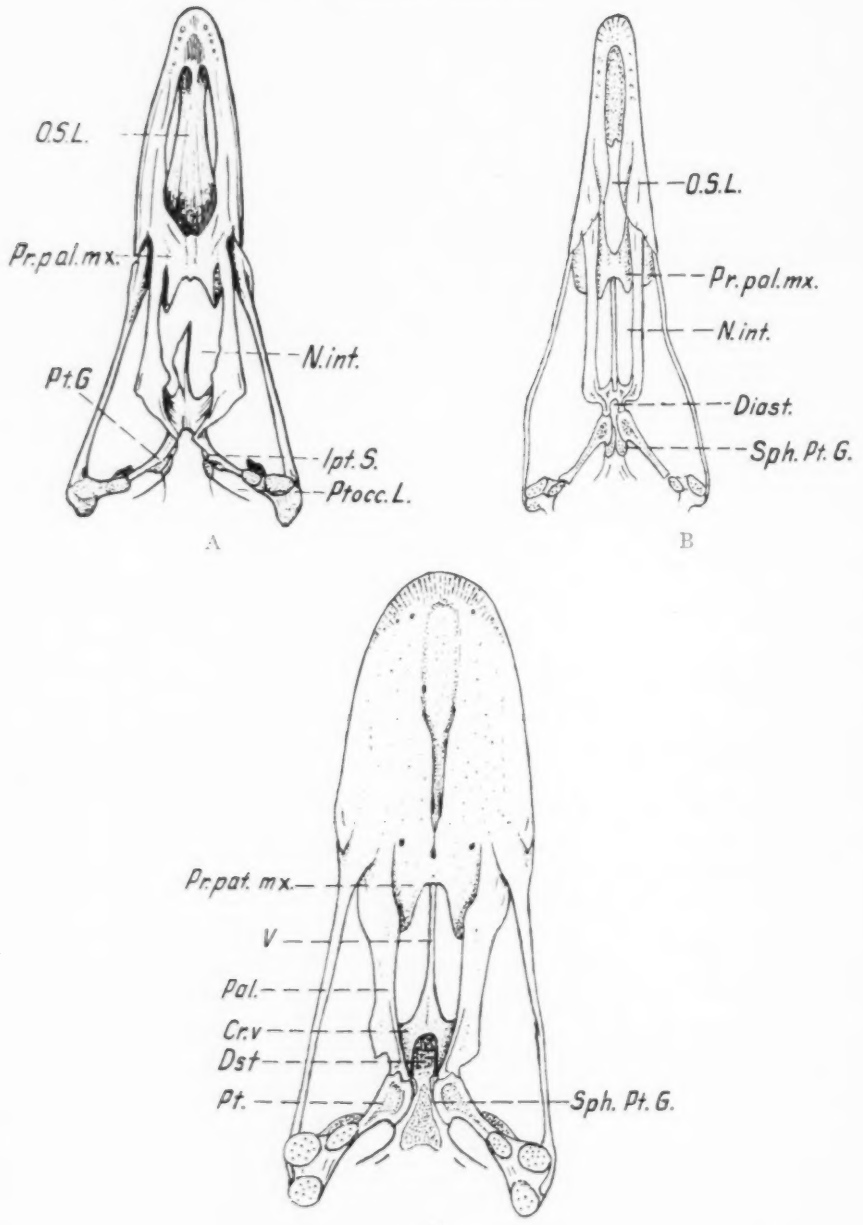

Abb. 6 A—C. Trennung des Choanenabschnittes von der Oberschnabellücke durch Bildung einer die beiden Kieferhälften verbindenden Knochenspange durch die Processus palatini maxillarum. A: *Chauna cristata*, umgezeichnet nach v. MARINELLI (1936). B: *Mergus albellus* (Orig.). C: *Cereopsis novae sealandiae* (Orig.). Bezeichnungen wie auf vorigen Abbildungen.

men, die den Schnabelteil der Gaumenlücke vom Choanenteil durch eine querverlaufende Knochenspange, gebildet von den Gaumenfortsätzen der Maxillaria, deren Caudalzipfel noch deutlich erkennbar sind, abgegliedert haben (Abb. 6). Ob dieser einfache und primitiv anmutende Zustand (*Chauna, Mergus*) auch phylogenetisch primitiv ist, wage ich nicht zu entscheiden, denn es wäre auch möglich, daß er durch sekundäre Ausweitung entstand. Das Bild, das Jungschädel von *Anser* zeigen, ähnelt stark dem Zustand, den wir bei der sehr altertümlichen *Cereopsis* finden. Der Gaumen läßt bei dieser Form noch deutlich den Umfang der beiden mächtigen Proc. palatini maxillarum erkennen, die sich nach der Mitte zu schieben und an der Berührungsstelle verschmelzen. Dadurch wird nicht nur der Choanenabschnitt der Oberschnabellücke vom Schnabelabschnitt geschieden, sondern auch letzterer weitestgehend eingeengt, wozu noch ein allmähliches Verknöchern von der Schnabelspitze her kommt. Anstelle eines ventral offenen sehen wir also einen durch einen knöchernen Boden weitgehend geschlossenen Oberschnabel. Einen solchen Verschluß der Schnabellücke finden wir auch bei den *Accipitres* (vgl. S. 230). Das ist der Grund, warum man annehmen könnte, daß derselbe Prozess auch bei den *Anseres* auf diese Weise vorsich ging. Dann aber wäre die vom Choanenabschnitt getrennte, selbst aber sehr weite Oberschnabellücke von *Chauna* und *Mergus* das Ergebnis einer sekundären Ausweitung. Das Problem wird durch den Gaumen von *Cygnus* nicht vereinfacht, denn dieser Typus (Abb. 3) läßt sich als Ergebnis eines weiteren Verschlusses der Gaumenlücke an den Typus *Mergus* und *Chauna* anschließen; der Gaumen des Jungtieres schließt sich aber an den Typus von *Anser* juv. und *Cereopsis* an. Die Frage, ob das Lückenmuster von *Chauna* und *Mergus* oder das von *Cereopsis* phylogenetisch primitiver ist, muß also offen bleiben. Hingewiesen sei noch darauf, daß die beiden inneren Nasenöffnungen durch den Vomer vollständig (*Mergus, Cygnus, Cereopsis*) oder unvollständig (*Chauna*) geschieden sein können. Ein Blick auf die bisher dargestellten Formen zeigt, daß die Oberschnabellücke aus zwei physiologisch verschiedenen Abschnitten besteht, die durch die Verschmelzung der Gaumenfortsätze der Maxillaria an ihrer Grenze geschieden werden können. Der Schnabelabschnitt der Oberschnabellücke ist eine Aussparung im Skelett, die so lange bestehen bleibt, als sie die Konstruktionsform des Schnabels nötig macht, dann aber verloren werden kann. Der Choanenabschnitt, der Mundhöhlenöffnung der Nase dienend, muß bei den Choanaten immer erhalten bleiben. Die Modifikationen der Schnabellücke werden also immer nur den rostralen Teil betreffen können, der auch die verschiedensten Befunde erheben läßt, während der Choanenabschnitt konservativ bleiben muß. Jedenfalls entsteht dadurch ein Lückentypus, der dem des Reptilschädels nicht mehr ähnlich ist und nur auf dem Umweg über den schizognathen, weitgehend geöffneten Gaumen auf den Reptilgaumen zurückgeführt werden kann.

Im Anschluß an die *Anseres* seien die *Cathartae* kurz erwähnt, die mit ihnen

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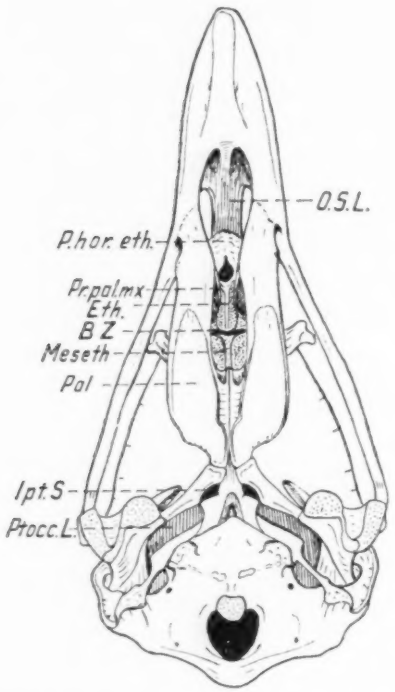

Abb. 7. Überbrückung der Oberschnabellücke durch das Ethmoidalskelett bei *Sarcorhamphus* (*Gypagus*) (Orig.). *Eth.* Ethmoid; *BZ* Beugungszone an der Schnabelbasis durch die Oberschnabellücke sichtbar; *Meseth* Mesethmoid; *P.hor.eth.* Pars horizontalis ethmoidei.

auch phylogenetisch im Zusammenhang stehen dürften. Die Skelettanatomie des Gaumens ist bei den Neuweltgeiern weitgehend einheitlich, so daß wir uns auf die Bearbeitung von *Sarcorhamphus* (*Gypagus*) beschränken können. Die Schnabellücke steht mit der infolge des Verlustes des Vomer einheitlich gewordenen inneren Nasenöffnung in breiter Verbindung (Abb. 7). Die maxillaren Gaumenfortsätze sind klein, löffelförmig und wenden sich scharf nach caudal und stehen untereinander nicht in knöcherner Verbindung. Das Gaumenskelett besitzt keine wechselseitigen Verbindungen seiner knöchernen Elemente; der Zustand ist also eindeutig schizognath (vgl. dazu PYCRAFT 1902). Die irrige Auffassung, die *Cathartae* seien desmognath, kommt daher, daß im Rostralabschnitt der Oberschnabellücke in der Tiefe eine querstehende Knochenplatte sichtbar ist, die nicht in der Gaumenebene selbst, sondern deutlich etwas tiefer die beiden Processus palatini maxillarum zu verbinden s c h e i n t. Diese Knochenplatte geht kontinuierlich in das hier knöcherne Septum nasi über und dient dazu, einen knöchernen Boden der Nasenkapseln zu bilden. Lateral steht diese Platte, die Pars horizontalis ethmoidei, mit den Maxillaria und ihren Gaumenfortsätzen in Verbindung, und zwar durch zwei Knochenspangen.

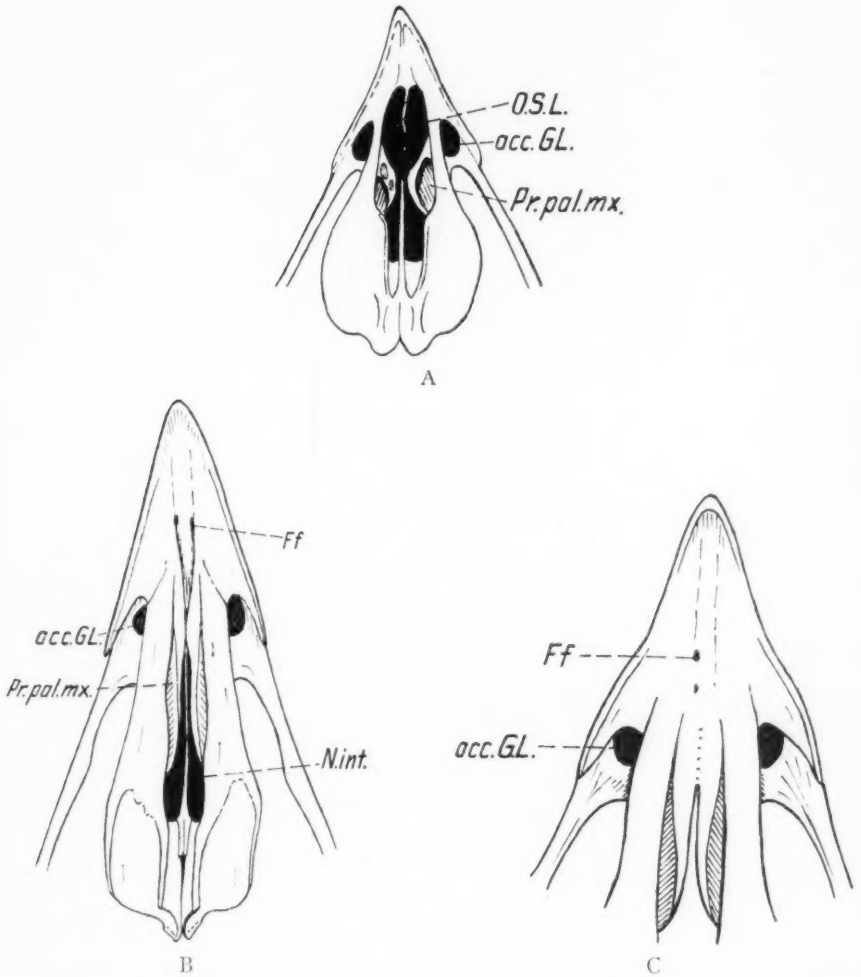

Abb. 8 A—C. Verschluß der Oberschnabellücke durch allmähliche Einengung durch den Processus palatinus maxillae bei den *Accipitres*. A: *Elanus sp.*, reine Schizognathie, weite Oberschnabellücke. B: *Aquila chrysaetos*, Oberschnabellücke praktisch bis auf den immer offen bleibenden Choanenraum geschlossen; Grenzfall von Schizo- und Desmognathie. C: *Accipiter nisus*, vollständiger Verschluß des Schnabelabschnittes der Oberschnabellücke bis auf einige Foramina; vollständige Desmognathie. Alle Fig. Originale. *Ff* Foramina.

Daraus eine Desmognathie konstruieren zu wollen, ist ganz verfehlt, denn ihr Kennzeichen ist die Verschmelzung der Gaumenfortsätze untereinander, was hier eben nicht zutrifft. Die Spangenverbindung des Ethmoidalskelettes mit den Maxillaria und ihren Gaumenfortsätzen ist auch keine Besonderheit der Neuweltgeier, sondern findet sich bei sehr vielen Vogelordnungen, bei denen der Nasenboden ossifiziert wird. Vergleicht man die *Cathartae* mit den

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Anseres, so ist evident, daß bei ersteren die Schnabellücke nicht unterbrochen, sondern durch das Ethmoidalskelett überbrückt wird.

Am häufigsten erfolgt der Verschluß der Oberschnabellücke durch allmähliche und allseitige Einengung. Als Beispiel eines solchen Vorgangen, der bei allen in Frage kommenden Vogelordnungen etwas anders verläuft seien die *Accipitres* erwähnt (PYCRAFT 1902, SHUSHKIN 1899), die alle Stufen der Ausbildung der Schnabellücke bis zu ihrem völligen Schwund zeigen. Die Spezialisationsreihe, keineswegs einer Stammreihe gleichzusetzen, beginnt mit *Elanus* (Abb. 8), der im Gaumenbau entschieden primitive Züge bewahrte. Die Schnabellücke steht in breiter Verbindung mit den durch einen Vomer geschiedenen Choanenabschnitten; die maxillaren Gaumenfortsätze sind relativ groß, löffelförmig, zeigen nach hinten und bleiben weit voneinander getrennt. Die meisten übrigen *Accipitres* zeigen ein Gaumenbild, das auf das eindeutig schizognathe von *Elanus* zurückgeführt werden (PYCRAFT, SHUSHKIN), in der Höhe der Differenzierung aber weitgehend verschieden sein kann. Der Verschluß der Schnabellücke geschieht durch starke Größenzunahme der Gaumenfortsätze der Maxillaria, die nicht direkt aufeinander zuwachsen, sondern in ganzer Länge in die Schnabellücke eindringen. An diesem von lateral und rostral her vordringenden Knochenwachstum dürften nicht nur die Maxillaria, sondern auch die Praemaxillaria beteiligt sein. Durch dieses gleichmäßige Vordringen des Knochens nach medial wird die Schnabellücke allmählich eingeengt und es kommt erst spät zur Berührung der beiderseitigen, stark pneumatisch aufgetriebenen Gaumenfortsätze der Maxillaria. Daher kann die Schnabellücke praktisch verschwunden sein, ohne daß ein desmognather Zustand eindeutig erworben ist (*Aquila*), was zu langatmigen Diskussionen Anlaß gab. Gleichzeitig mit dem Vordringen des Knochens von den Kieferrändern aus erfolgt eine bedeutende Größenzunahme des Septum nasi, so daß auch dieses die Schnabellücke, allerdings von der Mitte aus, zurückdrängt. Von dieser bleiben dann als Rest einige meist paarige Foramina übrig, bestenfalls ein Spalt (*Circactus*). Über diesen Zustand, der an der Grenze von Desmognathie und Schizognathie steht und noch deutlich den ursprünglichen Gaumentypus von *Elanus* erkennen läßt, führt die Entwicklung zu Formen, die rein desmognath sind und ihrerseits auf den Gaumen von *Aquila* zurückgeführt werden können. Die Verteilung dieser komplett desmognathen Formen im System ergibt mit Sicherheit, daß dieser Entwicklungsweg innerhalb der *Accipitres* mehrfach beschritten wurde. Wir nennen nur *Accipiter nisus, Falco peregrinus, Ibycter, Polyborus, Haliaetus* und *Aegypius*. Die Gaumenfortsätze sind bis auf die freien Caudalenden völlig verschmolzen, das Septum nasi ist als gesondertes Element meist nicht mehr erkennbar, von der Schnabellücke bleiben einige Foramina übrig, die bei den Falken im Zusammenhang mit dem Gaumenbeißkiel verschwinden.

Haben wir bisher dargelegt wie der primitive Lückentypus des schizo-

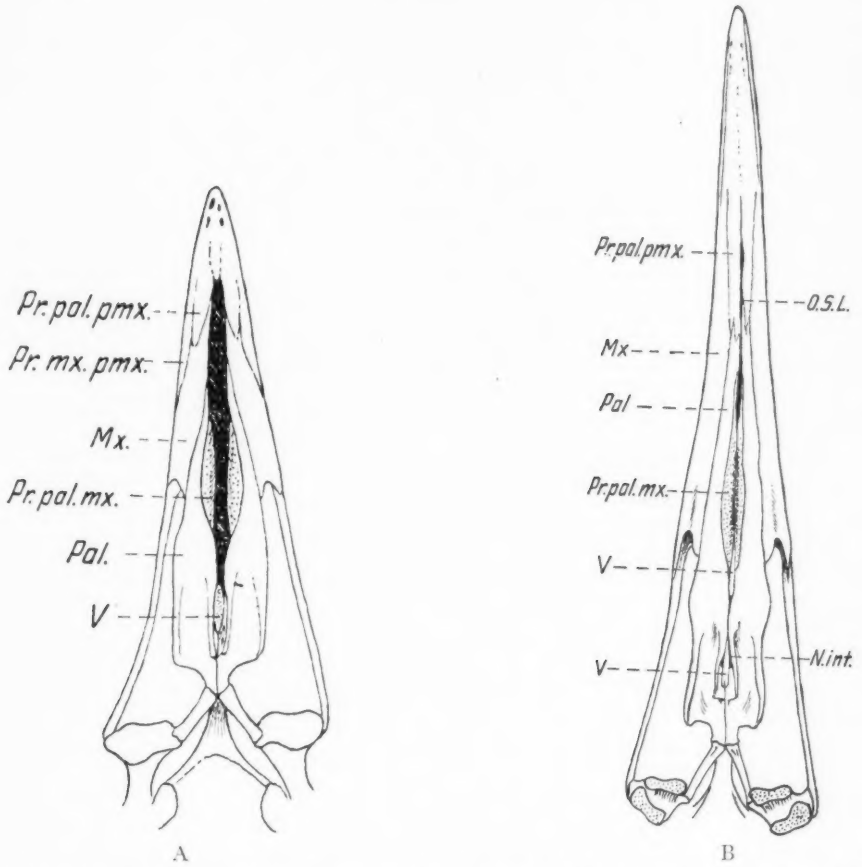

Abb. 9 A—B. Ontogenetischer Verschluß der Oberschnabellücke durch Vorwachsen des Processus palatinus maxillae beiderseits bei Störchen. A: *Abdimia*, Pullus. B: *Ciconia alba* juv. Vorgeschrittene Reduktion der Oberschnabellücke (Orig.). *Pr.mx.pmx.* Processus maxillaris praemaxillaris.

gnathen Gaumens in den abgeleiteten des desmognathen in Rahmen sicherer Verwandtschaftskreise übergeht, so soll nun derselbe Vorgang ontogenetish verfolgt werden. Man könnte es mit einem Hinweis auf diese längst bekannte Tatsache bewenden lassen, aber das Zoologische Institut der Universität Wien besitzt die seltenen Jungschädel von *Balaeniceps* und *Abdimia*, zwei Formen die im Alter eindeutig desmognath sind, und deren Bearbeitung von Interesse ist.

Der Schädel von *Abdimia* (Abb. 9) stammt von einem Pullus. Der Gaumen zeigt eine lange mit dem Choanenabschnitt in Verbindung stehende Oberschnabellücke, die von den typischen Knochen umgrenzt wird. Die Maxillaria sind wie bei allen Störchen groß; ihre Gaumenfortsätze engen die Schnabellücke

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stark ein, doch kommt es zu keiner Berührung auf diesem Stadium. Der Gaumen ist also eindeutig schizognath. Auffällig ist, daß bei *Abdimia*, ebenso wie bei *Ciconia* keine Basipterygoidgelenke entwickelt sind. Bei einem etwa gleichalten *Balaeniceps rex* — dasselbe Exemplar, das von BÖHM (1930) bearbeitet wurde —, sehen wir schon den nächsten Spezialisationsschritt. Die Maxillaria, auch hier sehr groß, entwickeln mächtige Gaumenfortsätze, die sich in der Medianlinie des Gaumens eben berühren (BÖHM 1930, S. 684 und Abb. 4). Zwar ist von einer Desmognathie noch nicht zu sprechen, aber die Trennung des Choanenabschnittes der Schnabellücke von ihrem Rostralabschnitt ist schon auf diesem Stadium vollzogen. Vergleicht man mit den beiden beschriebenen Schädeln den eines älteren Jungtieres von *Ciconia* (Abb. 9), der nur mehr im Bereiche des Maxillarsegmentes Knochennähte zeigt, so erkennt man sofort die vermittelnde Stellung dieses Stadiums. Die Gaumenfortsätze der Maxillaria haben beträchtlich an Größe zugenommen und drängen die Oberschnabellücke, die vom Choanenabschnitt schon getrennt ist, bis auf einen unregelmäßigen schmalen Spalt zusammen. Auch hier ist die Frage, ob man noch von Schizo- oder schon von Desmognathie reden soll weniger wichtig, als die Feststellung, daß der Verschluß der Gaumenlücke durch langsames Vorwachsen der Gaumenfortsätze der Maxillaria erreicht wird. Es ist also ontogenetisch derselbe Prozess, wie er bei den *Accipitres* in Spezialisationsreihen erwachsener Stücke zu verfolgen war. Ebenso bieten auch die erwachsenen Stadien der hier behandelten Störche manche Parallelen zu den Raubvögeln. Das Lückenmuster entspricht dem des desmognathen Gaumens. Bei *Balaeniceps* scheint der Vomer geschwunden zu sein; die Choanenöffnung ist daher am Skelettschädel unpaar (Abb. 10). Die Gaumenfortsätze der Maxillaria, völlig eingeschmolzen in den knöchernen Schnabelboden, lassen häufig eine Verwachsungsnaht in Spuren noch erkennen. Im Bereiche der Processus palatini maxillarum treten häufig unregelmäßige Foramina auf, die als Reste der Oberschnabellücke gedeutet werden könnten. Von *Abdimia* liegt mir nur ein Stück vor, dessen Gaumen weitestgehend dem von *Ciconia* gleicht. Bei letzterer ist am erwachsenen Gaumen ein beträchtliches Variieren in der Reduktion der Oberschnabellücke festzustellen. In den bei weitem zahlreichsten Fällen ist sie noch durch vermehrtes Vorkommen teilweise zusammenfließender Foramina erkennbar, doch sind die Gaumenfortsätze immer verschmolzen. Vielfach ist der dem Processus palatinus maxillae zuzurechnende Knochen durch seine geringere Dichte von dem der Palatina und Maxillaria unterschieden. Oft treten rostral der verschmolzenen Gaumenfortsätze der Maxillaria noch Öffnungen auf, die der Oberschnabellücke entsprechen (*Ciconia nigra*, Abb. 10). Bei dem ziemlich umfangreichen Material an Storchschädeln, das mir zur Untersuchung vorlag, gewann ich den Eindruck, als sei ein zweiter rückläufiger Process angebahnt, die sekundäre Wiedereröffnung des geschlossenen Schnabelbodens. Der Grund zu dieser Annahme ist, daß bei langen, spitzen

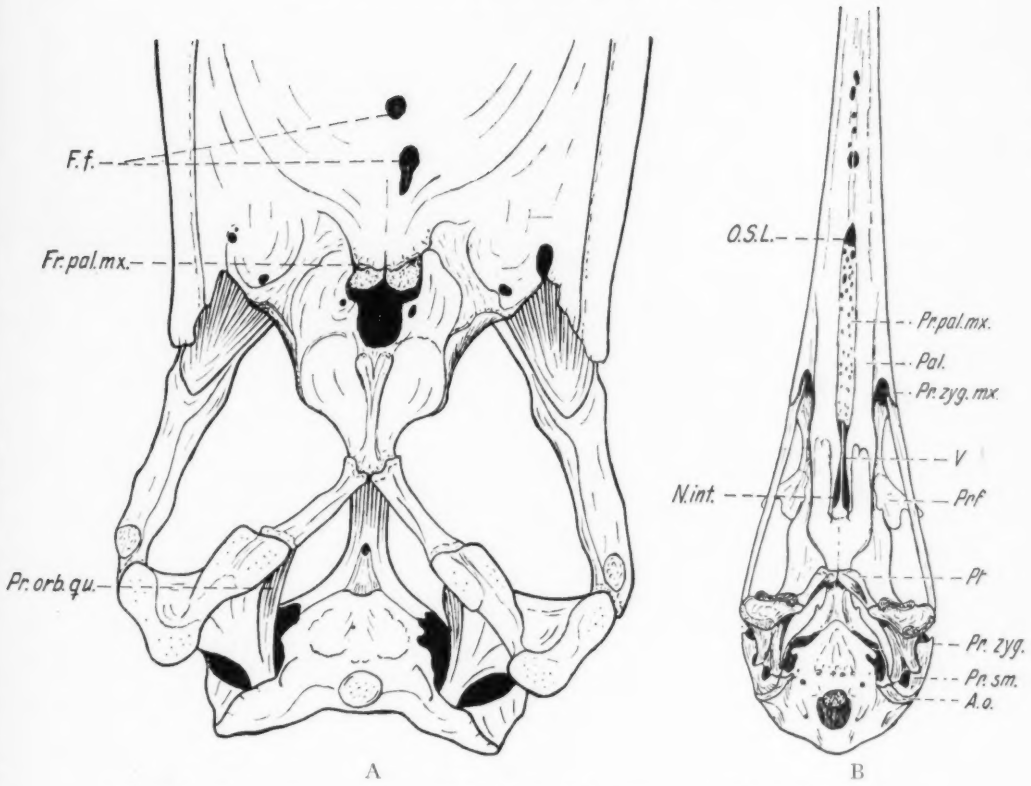

Abb. 10 A—B. Gaumen erwachsener Störche. A: *Balaeniceps rex* (Orig.). B: *Ciconia nigra* (Orig.). *A.o.* Ala occipitalis; *Pr.orb.qu.* Processus orbitalis quadrati; *Pr.sm.* Processus suprameaticus; *Pr.zyg.* Processus zygomaticus des Squamosum; *Pr.zyg.mx.* Processus zygomaticus maxillaris.

Schnäbeln, die zum kräftigen Zugreifen mit der Spitze verwendet werden, eine gewisse Biegsamkeit in der Medianebene nötig werden kann. Das kann einmal dadurch erreicht werden, daß das Praemaxillare nicht völlig mit dem Maxillare und Nasale verschmilzt, also etwas verschieblich bleibt; solche Schädel fanden sich bei *Leptoptilos*. Zum anderen kann es durch geringe Biegsamkeit im Schnabelfirst erreicht werden. Für letzteren Fall ist es günstig, wenn durch ein weites caudales Ausgreifen der Nasenlöcher der First gesondert wird — das wäre das Prinzip des schizorhinen Oberschnabels —; gerade das ist innerhalb der Variationsbreite bei *Ciconia* anzutreffen. Ist der Schnabelfirst etwas nachgiebig, so würde solchen schwingenden, vermutlich nur passiv ausgelösten Bewegungen, ein starr geschlossener Schnabelboden, wie er durch knöchernen allseitigen Verschluß der Oberschnabellücke entsteht, entgegenwirken. Vorläufig ist ein sicheres Urteil darüber noch nicht möglich, doch vermute ich, daß hier eine Umbildung in statu nascendi zu verfolgen wäre.

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Eine Veränderung an der knöchernen Umrahmung der Choanen ist zu erwähnen, die zwar nicht häufig ist, aber doch eine auffällige Anordnung von Munddachöffnungen bietet und einen Einblick in die durchgreifenden Zusammenhänge zwischen Schädelgestaltung und Kiefermechanik gestattet.

Bei *Steatornis* (*Caprimulgidae*) verschmelzen die ventralen Medialkanten der Palatina, etwa in Höhe der Vomerspitze, so daß die Choanen rostroventral von den Palatina umgriffen werden. Dadurch entsteht eine neue mittlere Gaumenlücke, die rostral von den verschmolzenen Processus palatini maxillarum, lateral und caudal von den Palatina umschlossen wird. Diese mittlere Gaumenlücke ist ein Rest der vor der Erwerbung der Desmognathie vorhandenen ausgedehnten Oberschnabellücke, deren caudalem Teil sie entspricht, den wir, läge die ungewöhnliche Verschmelzung der medialen Ventralkanten der Palatina nicht vor, dem Choanenabschnitt zugerechnet hätten. Ein ganz ähnliches Verhalten zeigen einige *Buccrotidae* und *Rhamphastidae*. Bei *Bucorvus* (*Tmetoceros*) *abyssinicus* (Abb. 11) sind ebenfalls die ventromedialen Kanten der Palatina verschmolzen, wodurch wieder ein innerer Rostralabschluß der inneren Nasenöffnungen bewirkt wird. Rostral dieser von den Palatina gebildeten Knochenbrücke findet sich noch ein Paar ovaler Öffnungen, das noch nicht im Schnabelbereich des Gaumens liegt und das als Rest der ehemals weiteren inneren Nasenöffnungen zu gelten hat. Eine unregelmässige Durchbrechung des sonst knöchern verschlossenen Schnabelbodens ist als Rest der ehemals weiten Oberschnabellücke anzusehen. Die Knochenbrücke, die zwischen der unpaaren rostralen und den paarigen caudalen Gaumenöffnungen, die wir beide auf die Oberschnabellücke zurückführten, zu finden ist, halten wir für den Verschmelzungsteil der Gaumenfortsätze der Maxillaria. Etwas andere, aber doch ganz ähnliche Verhältnisse zeigen auch andere *Buccrotidae*, wie eine Durchsicht unseres Skelettmateriales zeigt; vgl. dazu die Abb. bei STARCK (1940). Ein abschließendes Urteil ermöglicht sich erst nach Untersuchung von Jungtieren. STARCK (l. c. S. 611) bezeichnet die paarigen, rostral der Choanen liegenden Gaumenöffnungen als Foramina pneumatica, was sie der Funktion nach sein mögen, auch wenn man sie morphologisch als Reste der Gaumenlücke des Schnabels auffassen kann. Bei *Rhamphastos* trifft man auf ganz ähnliche Bedingungen wie bei den *Buccrotidae* (HUXLEY 1867, S. 444; HOFER 1945 a, S. 41).

Wie ist die Entstehung einer neuen, die beiden Palatina ventral verbindenden Knochenbrücke zu erklären? Das Palatinum bildet in seinem Caudalteil meist drei verschieden stark entwickelte Cristae aus (Abb. 2, *Otis*); die Crista dorsalis, an deren Aufbau sich vielleicht auch das Hemipterygoid beteiligt, bildet die Fläche, mit der das Palatinum am Rostrum sphenoidale gleitet. Meist setzt auf dieser Crista rostral der Vomer auf. Die laterale und ventrale Crista sind in verschiedenem Ausmaße an der caudalen löffelförmigen Verbreiterung beteiligt, die die Ursprungsflächen für den dorsalen und ventralen M. ptery-

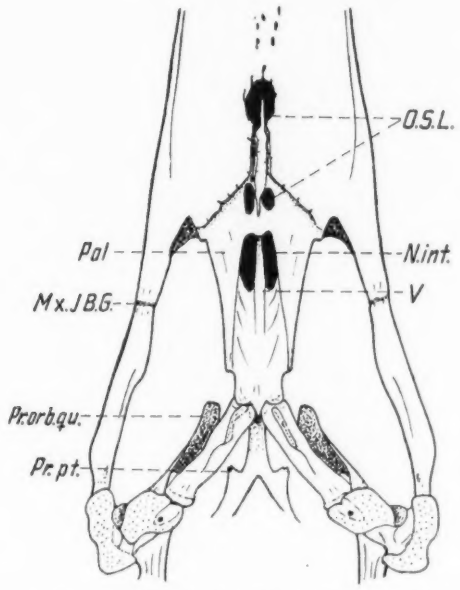

Abb. 11. Sekundäre rostrale Umrahmung der Nares internae durch Palatina bei *Tmetoceros* (*Bucorvus*) *abyssinicus* (Orig.). *Mx.JB.G.* Abgliederung des Jochbogens; *Pr.pt.* Processus pterygoideus basisphenoidei.

goideus abgibt. Die ventrale Crista schiebt sich zwischen den Medialrand des genannten ventralen Muskels und die Choane. Das die inneren Nasenöffnungen reichlich umgebende und den Muskel umkleidende Bindegewebe ist sehr maßgeblich an der Formung der ventralen Crista beteiligt, denn diese zeigt oft (*Corvus*, Abb. 5) eine leichte mediale Biegung, die durch die Form des Muskels nicht verständlich wird, wohl aber, wenn sie als Verknöcherung im Bindegewebe aufgefaßt wird. Dann umfaßt die Crista auch etwas von rostral die Choane. Besonders deutlich findet sich die mediale Wendung der ventralen Crista bei *Leptoptilos*. Die ventralen Cristae sind wechselseitig durch Bindegewebspolster verbunden, in denen eine Ossifikation möglich ist. Läßt man eine solche bei *Corvus* oder *Leptoptilos* eintreten, so verbinden sich die beiden Ventralcristae durch eine schmale Knochenbrücke und ein Zustand, wie er für *Steatornis, Bucerotidae* und *Rhamphastidae* beschrieben wurde, läge vor. Wir können diese Annahme umso leichter machen, als sich bei *Rhamphastos* ein solcher Spezialisationsweg aus der individuellen Variation zusammenstellen läßt. Huxley (1867) fand Stücke dieser Gattung, die eine solche wechselseitige Verbindung der ventralen Palatincristae zeigten, während ich selbst keine auffinden konnte. Allerdings ist die Erwerbung einer solchen knöchernen und damit starren Verbindung der beiden Palatina untereinander nur dann möglich, wenn die beiderseitigen Palatina keine selbständigen Bewegungen, und

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seien sie noch so geringfügig, ausführen können. Wir finden daher eine solche Knochenbrücke nur bei Formen die sympalatin sind, so daß Sonderbewegungen der Palatina ausgeschlossen sind. Umgekehrt erblicke ich darin einen Beweis, daß tatsächlich bei nicht sympalatinen Formen Sonderbewegungen der Palatina möglich sind und vorkommen. *Steatornis*, die *Bucerotidae* und *Ramphastidae* sind eindeutig sympalatin.[1]

Schließlich wenden wir uns den durch einen palaeognathen Gaumen gekennzeichneten Formen zu. Eine Diskussion über die Berechtigung seiner Unterscheidung, seine Spezialisationshöhe und morphologische Bewertung ist hier unnötig und würde auch keine Klärung in dieses noch weiterer Untersuchung harrende Problem bringen (Lowe 1928, Stresemann 1933, Gregory u. Murphy 1933—34, Marinelli 1936, Hofer 1945 a, McDowell 1948). Unter den palaeognathen Formen werden *Dromaius* und *Rhea* und die *Crypturi* allgemein im Gaumenbau als die am wenigsten spezialisierten angesehen. Bei den *Crypturi*, wir haben *Rhynchotus* und *Tinamus* im Auge, sind die Nares internae voneinander, aber auch von der Oberschnabellücke, durch den mächtig entwickelten Vomer geschieden (Abb. 12). Der Vomer, caudal den Pterygoidea aufsitzend, bildet eine in der Längsrichtung verlaufende, dorsal offene Rinne, in der das Rostrum sphenoidale gleiten kann. Er ist rostral gegabelt, zwei Praemaxillarfortsätze entwickelnd, die an ihrer Basis auseinanderstreben und dann rein nach vorne ziehen. Sie liegen dorsal den nach caudal strebenden Processus palatini praemaxillarum an, verschmelzen jedoch nicht mit ihnen. Die Oberschnabellücke ist also in getrennte Choanenabschnitte und Schnabelgaumenlücke durch den Vomer geschieden. Die verbleibende Oberschnabellücke wird nur von Vomer und Praemaxillare umrahmt und weicht hierin von der entsprechenden Lücke neognather Formen ab (*Mergus*, *Chauna*, Abb. 6). Daß von ihrer Umrahmung auch das Maxillare ausgeschlossen bleibt, ist in erster Linie auf die mächtige Entwicklung von Vomer und Palatinum zuryckzuführen und ist nicht charakteristisch für den palaeognathen Gaumen (*Struthio*, *Apteryx*). Ein Gaumenfortsatz des Maxillare ist, soweit an dem mir vorliegenden Skelettmaterial zu sehen ist, bei den *Crypturi* nicht entwickelt. Pycraft (1900, S. 187) meint, daß das Maxillare der *Crypturi* dem von *Rhea* ähnlich sei; der Processus palatinus maxillae sei schwächer und nicht gefenstert. Die Beobachtung eines solchen Fortsatzes durch Huxley (1867, *Tinamus*) konnte ich nicht bestätigen. Dadurch werden die inneren Nasenöffnungen bei *Tinamus* nur von Vomer und Palatinum umschlossen; rostral kann in sie der Caudalzipfel des Palatinfortsatzes des Praemaxillare hineinragen.

Rhea weist ein den *Crypturi* weitgehend ähnliches Lückenmuster auf. Die einzige Veränderung bedingen die breiten, muscheligen, teilweise durchlöcher-

[1] Ausserdem sind diese Formen desmognath und stützen damit meine früher aufgestellte Behauptung (1945 a, S. 146), daß die Sympalatinie mit der Desmognathie gekoppelt sei. Über den Sonderfall der *Striges* vgl. l. c. S. 146 und diese Arbeit S. 220.

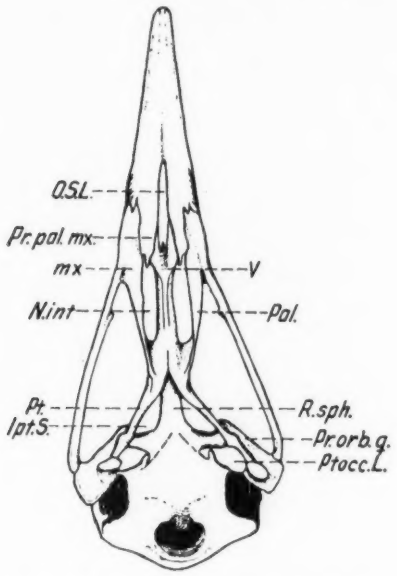

Abb. 12. Lückenmuster eines primitiven neognathen Gaumens. *Tinamus* sp. nach einer unveröffentlichten Abbildung v. MARINELLIS umgezeichnet.

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ten Processus palatini maxillarum, die an der Umrahmung der Choanenöffnung teilhaben. Die Gaumenfortsätze der Maxillaria schließen an die der Praemaxillaria an und überlagern sie etwas von dorsal, jedoch kommt es zu keiner Verschmelzung. *Rhea* ist ebenso wie die *Crypturi* rhynchokinetisch.

Von *Dromaius* und *Casuarius*, die einander im Gaumenlückenmuster sehr ähnlich sind, besprechen wir nur letzteren (Abb. 13). Die ursprüngliche Gaumenlücke ist auch hier in einen sehr weit rostral liegenden kleinen Schnabelteil und die beiden mächtigen Choanen geschieden. Der Vomer ist schmal und wesentlich schwächer als bei den anderen Palaeognathen; auch seine Anlehnung an das Rostrum sphenoidale ist weniger intensiv als bei jenen. Das spricht gegen eine ausgeprägte und ausgiebige Schädelkinetik. Abweichend ist die Oberschnabellücke. Die Gaumenfortsätze der Praemaxillaria und Maxillaria und der Vomer bilden eine breite Platte, die etwas nach ventral durchgebogen ist. Diese Platte ist durch eine schmale und kurze Lücke nahe der Schnabelspitze durchbrochen. Das mir vorliegende Stück zeigt keine Grenze zwischen dem Vomer und den Gaumenfortsätzen des Praemaxillare. PYCRAFT (1900, S. 188) beschreibt den Vomer bei *Casuarius* folgendermaßen: „Anteriorly the vomer becomes laminate and wedged in between the maxillo—palatine processes (Processus palatinus maxillae unserer Terminologie), and passing forwards rests upon the palatine processes of the praemaxilla." Daß bei Casuarius beide Grenzfälle verwirklicht werden können, die Verschmelzung

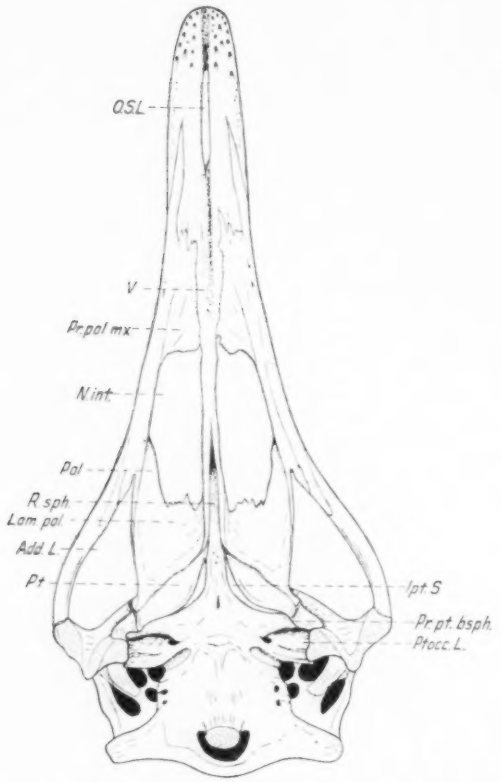

Abb. 13. Gaumen von *Casuarius* sp. fem. (Orig.). Beachte die weit rostral liegende Oberschnabellücke. Vomer schwach. *Lam. pal.* Gaumenlamelle des Palatinum.

zwischen Vomer und Processus palatinus des Praemaxillare ebenso, wie die Trennung beider Bildungen, spricht gegen eine ausgiebige Rhynchokinetik, denn nur eine solche käme in Frage. Ein von mir auf seine Muskulatur hin untersuchter Schädel von *Casuarius* ließ auch deutlich erkennen, daß die einzigen Bewegungen die im Schädel möglich sind, passiv durch ein nicht ausgiebiges Nachgeben der Firstspange des Oberschnabels sowie des rostralen Teiles des Munddaches erfolgen und durch Schnabelstöße ausgelöst werden.

Wirkte der Oberschnabelabschnitt des Gaumens bei *Casuarius* schon weitgehend geschlossen, so ist das in erhöhtem Maße bei *Apteryx* der Fall. Der gestreckte Schnabel wird als Knopfsonde verwendet; er ist im apikalen Drittel sehr biegsam. Das an der Schnabelspitze gelegene Geruchsorgan bedarf eines Schutzes von ventral, den es durch den knöchern verschlossenen Schnabelboden erhält. Hierin liegt ein Unterschied zwischen dem Schnabel des Kiwis und dem sonst so ähnlichen Schnabel von *Scolopax* (Marinelli 1928). Bei letzterer sind die Maxillarspangen dünn und biegsam, die Gaumenlücke des Ober-

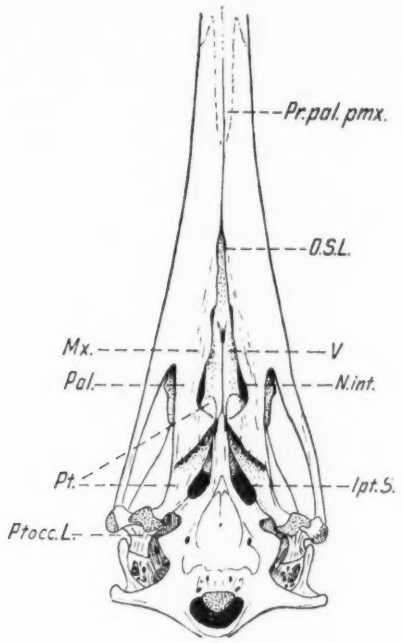

Abb. 14. Gaumen von *Apteryx australis*. Fast völlige Reduktion der Oberschnabellücke (Orig.).

schnabels reicht bis fast zur Schnabelspitze. Ein knöcherner Verschluß des Gaumens im Rostralteil des Schnabels könnte durch das Geruchsorgan nicht erklärt werden, da dieses typisch an der Basis des Schnabels liegt, wie immer bei Vögeln. Beim Kiwi (Abb. 14) sind die inneren Nasenöffnungen längsovale Schlitze, breit geschieden durch den sehr mächtigen Vomer. Lateral werden sie durch das Palatinum umrahmt, das eine ventromedial gerichtete Lamelle entwickelt, die die Choane etwas überdeckt. Ebenso wie bei *Casuarius* und *Dromaius* (Abb. 15) kommt es zum Kontakt zwischen dem umfangreichen Maxillare und dem Vomer rostral der Choanen, doch bildet sich keine Nahtverbindung. Der Vomer ist rostral schwach gekerbt, doch finden sich keine ausgesprochenen Processus praemaxillares wie bei *Rhea*. Etwas deutlicher sind sie bei *Dromaius* juv. Rostral des Vorderendes des Vomer findet sich eine schmale, pfeilspitzenähnliche Öffnung, die lateral und rostral von den mächtigen Gaumenfortsätzen — besser wäre von Gaumenplatten die Rede —, der Maxillaria eingefaßt wird. Es ist der Rest der Oberschnabellücke, die von Vomer und Maxillare umrahmt wird; man beachte, daß hier genau das Gegenteil des bei *Tinamus* gefundenen Zustandes vorliegt, wo die Oberschnabellücke durch Vomer und Praemaxillare umschlossen wurde. Bei *Apteryx* erreichen die Caudalenden praemaxillaren Gaumenfortsätze nicht einmal das Rostralende der

Oberschnabellücke. Letztere setzt sich nach rostral in einen allmählich zulaufenden und sich verlierenden Schlitz fort, der zwischen die Gaumenplatten der Maxillaria eindringt. Die mir vorliegenden Stücke zeigen nur stellenweise noch Reste der das Palatinum und Maxillare trennenden Naht.

Das Gaumenbild von *Struthio* ist wesentlich verschieden von dem des Kiwis. Bei letzterem ist das Entwicklungsziel offensichtlich der möglichste Verschluß der Gaumenlücken, bei ersterem ihre nur irgend erreichbare Erweiterung um zu einem Spangenbau des Gaumens zu gelangen. Dadurch kommt *Struthio* in eine Sonderstellung, deren Abstand jedoch durch das Gaumenskelett des Foetus überbrückt wird. Dieses konnte an einem noch in der Eischale befindlichen, schlüpfreifen Tierchen untersucht werden.

Beim erwachsenen Strauß (Abb. 16) sind die einzigen plattenartig entwickelten Gaumenknochen das Pterygoid und die Gaumenfortsätze des Maxillare. Letztere verbinden sich medial durch sehr festen Kontakt mit dem Vomer und trennen so den Schnabelabschnitt der Gaumenlücke von ihrem Choanenteil, der seinerseits wieder völlig durch das Rostrum sphenoidale und den Vomer geschieden wird. Gaumenfortsätze der Praemaxillaria fehlen dem erwachsenen Tier, so daß die Oberschnabellücke außerordentlich weit wird. Die schmalen, spangenartigen Palatina zeigen nur zipfelartige Horizontallamellen, die von caudal und lateral in die Choanen hineinragen. Im Verhältnis zum Foetus haben die Maxillaria beträchtlich an Umfang eingebüßt. Kräftig entwickelt sind nur die Gaumenfortsätze derselben, die sich gegen den Vomer stemmen, der seinerseits seine Verbindung mit den Pterygoidea aufgegeben hat und auf dem stark pneumatisierten Rostrum sphenoidale gleitet, welches er von ventral umfaßt. Soweit mir bekannt ist, wurde noch kein Stadium bei *Struthio* gefunden, bei dem der Vomer noch die ursprünglich sicher vorhandene direkte Verbindung mit den Pterygoidea zeigt. MARINELLI hat, nach mündlicher Mitteilung, straffe Bindegewebszüge bei erwachsenen Straußen gefunden, die die caudal frei endigenden Vomerschenkel mit den Rostro-Medialkanten der Pterigoidea verbinden. Denselben Befund konnte ich an dem Foetus erheben. Durch die starke caudale Reduktion des Vomer in der Stammeslinie von *Struthio* kommt das Rostrum spheniodale in die Lage, die Nares internae am Skelettschädel wenigstens teilweise medial zu begrenzen. Infolge der durch die Reduktion der Gaumenfortsätze der Praemaxillaria bedingten weiten Eröffnung der Schnabellücke wird diese vom Corpus praemaxillaris, Maxillare, Rostralteil des Palatinum und Vomer umschlossen.

Dieses völlig abweichende Gaumenbild des erwachsenen Straußes vergleichen wir dem des Foetus (Abb. 15). Auch D'ALTON (1827) untersuchte einen dem Ei entnommenen Foetus von *Struthio*. Seine Abbildung und Beschreibung stimmen mit den meinigen völlig überein; lediglich die accessorischen Gaumenlücken sind etwas größer. Außerdem ziehen wir die Bearbeitung eines Embryos des Straußes durch PARKER (1866) heran, bei dem die Knochenbildung

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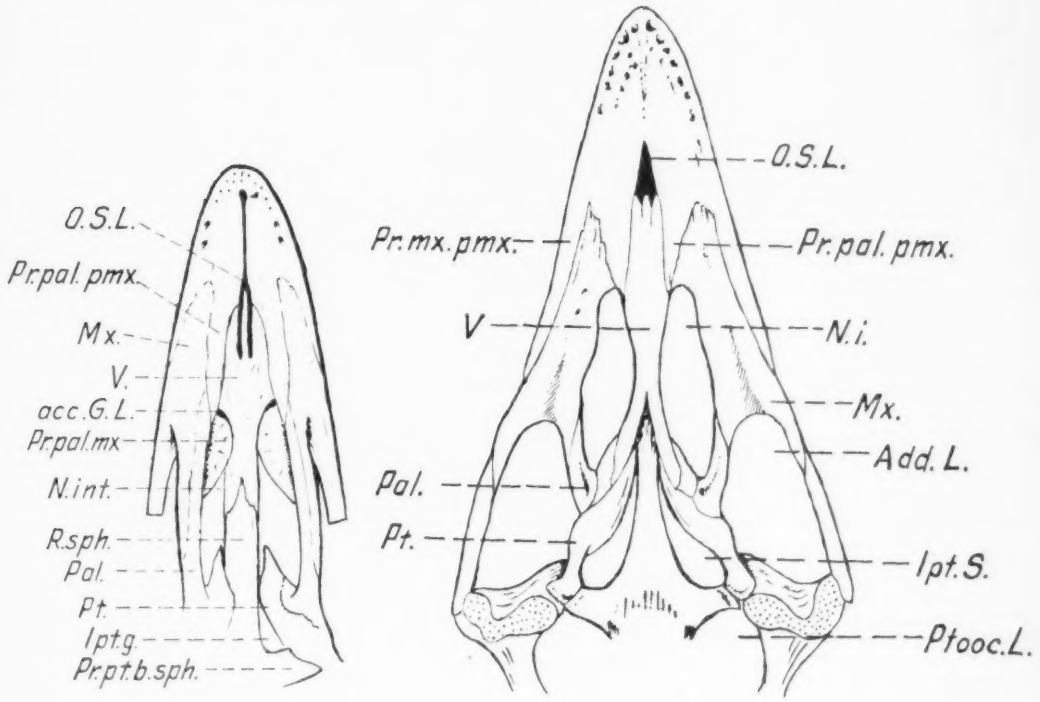

Abb. 15. Palaeognathengaumen im Foetalzustand. A: *Struthio* sp. dem Ei entnommen; B: *Dromaius* nach PARKER (1866). A Original. Der Kopf von *Struthio* konnte nicht vollständig dargestellt werden, da er schon zur Muskelpräparation verwendet war und dabei in der Quadratregion zerstört wurde.

eben begonnen hatte, der also etwas jünger war als der hier untersuchte. In folgenden Punkten zeigt sich die tiefgreifende Veränderung, die der Straußengaumen in seiner Ontogenie mitmachen muß; hierin zeigt sich auch die mit den Gaumenbildern der anderen Ratiten vermittelnde Stellung des Foetus.

1) Das Praemaxillare besitzt einen bedeutenden Processus palatinus, der von lateral die Schnabellücke eingrenzt und caudal mit den Maxillaria und Palatina in Verbindung steht. Damit weicht das Praemaxillare des foetalen Straußes nicht von dem der anderen Vögel prinzipiell ab.

2) Der Vomer zeigt die auffallendsten Veränderungen. Die caudale Verbindung mit den Pterygoidea fehlt, jedoch wird rostral jederseits ein Processus praemaxillaris entwickelt, der sehr ähnlich dem von *Rhea* die Gaumenfortsätze der Praemaxillaria überlagert. Außerdem besitzt er einen langen in die Oberschnabellücke hineinreichenden rostralen und sehr dünnen Medianfortsatz, den man andeutungsweise auch bei *Rhea* und den *Crypturi* finden kann; deutlicher ist er beim Embryo von *Dromaius*. Abgesehen von seiner caudalen

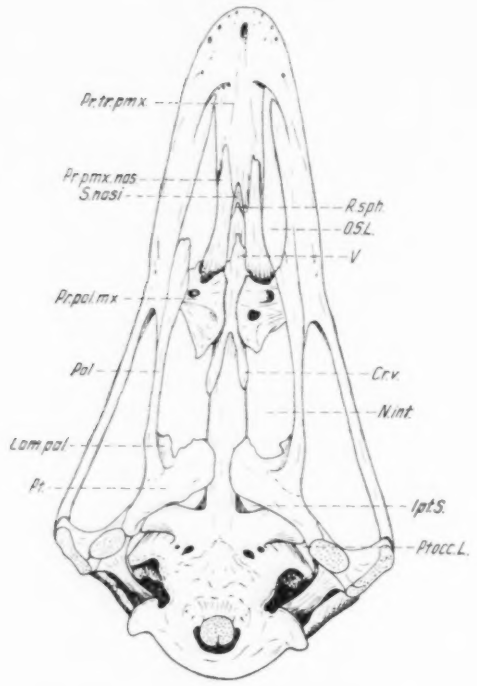

Abb. 16. Gaumen von *Struthio camelus* adult (Orig.). Vergleiche mit dem Gaumenbild des Fötus Abb. 15.

Verkürzung hat der Vomer eine außerordentlich ursprüngliche Form in Foetalzustand erhalten.

3) Die durch die bisher beschriebenen Knochen eingeengte Oberschnabellücke schließt den Gaumentypus des fötalen *Struthio* an die anderen Palaeognathen an. Ihre sekundäre Ausweitung erfolgt erst nach dem Schlüpfen, dürfte dann aber sehr schnell vorsich gehen, denn ein 7,5 cm langer Schädel eines Jungstraußes, bei dem die Ossifikation noch lange nicht ihr endgültiges Ausmaß erreicht hat, zeigt schon die vom adulten Tier her bekannte Oberschnabellücke.

4) Die Pterygoidea erinnern schon stark an den adulten Zustand, doch entwickeln sie rostro-medial zwei kräftige nach oral strebende Spitzen, die den Vomer zwar nicht erreichen, aber wohl als Reste der ursprünglichen Knochenverbindung angesehen werden können. Die auch hier gefundenen straffen Bindegewebszüge wurden schon erwähnt. In diesem Zustand ist das Pterygoid infolge seiner weiteren rostralen Erstreckung dem der anderen straußenartigen Vögel sehr ähnlich, insbesondere dem von *Dromaius* und *Casuarius*.

An den Gaumen des erwachsenen Straußes erinnert schon der fötale Processus palatinus maxillae. Zwischen ihm und dem Lateralrand des Vomer blei-

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ben kleine accessorische Gaumenlücken frei, die bei der allmählichen Reduktion des Rostralteiles des Vomer in die Oberschnabellücke mitaufgenommen werden.

c. *Adductorlücke und accessorische Gaumenlücken.*

Damit wenden wir uns der größten Öffnung des Gaumens zu, die wir in ähnlicher Form schon beim Reptilschädel fanden, wo sie meist „untere Schläfenöffnung" genannt wird. Damit soll gesagt werden, daß sich am Skelettschädel durch diese Lücke die Schläfengrube nach unten öffnet, so wie sie sich durch getrennte Fenster am Schädeldach nach dorsal und lateral öffnen kann. Zwischen diesen drei Schläfenöffnungen besteht jedoch ein genetischer Unterschied; das dorsale und laterale Fenster sind Durchbrechungen des ehemalig geschlossenen Schädelpanzers, für deren teilweise phylogenetisch zu verfolgende Entstehung funktionelle Gesichtspunkte erläuternd herangezogen wurden (Versluys 1936, hier weitere Literatur). Hingegen ist die sogenannte untere Schläfenöffnung, Lakjers Hinterseitenspalt, vom Fischkopf auf den Tetrapodenschädel übertragen worden und dient in beiden Gruppen dem Durchtritt der Adductorenmuskulatur. Daher ist die untere Schläfenöffnung eine bauplanmäßige Aussparung im Wirbeltierschädel und nicht eine später auftretende, nur auf einen Stamm beschränkte Durchbrechung, wie die dorsale und laterale Schläfenöffnung. Wir wollen diese Öffnung Adductorlücke nennen und damit zum Ausdruck bringen, daß sie phylogenetisch und funktionell eben etwas anderes ist als eine Schläfenöffnung.

Bei den Vögeln zeigt die Adductorlücke keine Besonderheiten. Sie wird medial und caudal von Elementen des Palatoquadratum, lateral aber von solchen des Jochbogens (Quadratojugale, Jugale, Processus jugalis maxillae), die Reste des ehemaligen Schädelseitenpanzers darstellen, umrahmt; rostral wird sie vom Maxillare umschlossen. Durch den Verlust des Transversum bei den Vögeln ist die laterale Gaumenlücke der Reptilien mit der Adductorlücke vereint worden. Die Adductorlücke der Vögel ist also das Homologon der Adductorlücke + laterale Gaumenlücke der Reptilien. Eindeutig scheint das durch das Nervenverhalten bewiesen, denn der Trigeminuszweig, der bei den Reptilien durch die laterale Gaumenlücke durchtritt, findet sich bei *Rhea* in der Adductorlücke (Boas 1914).

Das Transversum zieht bei Reptilschädeln vom Rostralende des Pterygoid an das Caudalende des Maxillare, die laterale Munddachlücke von der Adductorlücke scheidend. Es bildet einen caudomedialen Pfeiler des Maxillare, der vor allem dann wichtig wird, wenn der untere Jochbogen reduziert wurde (Abb. 1). Sein Verlust bei den Vögeln ist deshalb auffällig, weil damit dem Maxillare eine Stütze genommen wird, deren es scheinbar bedarf, denn die Desmognathie erklärt sich funktionell daraus, daß die beiden Kiefer caudal und medial versteift werden müssen. Der Zusammanhang, der den Verlust des

Transversum verstehen läßt, ist die Vergrößerung der Augen im Vogelstamm, die schon bei den *Pseudosuchia* beginnt und bei *Archaeornis* ein beträchtliches Ausmaß erreicht hat. Das Auge füllt bei den Vögeln nicht nur die ganze Orbita aus, sondern reicht mit seinem ventralen Umfange bis in die Höhe des Jochbogens, meistens sogar etwas darunter. Das Transversum läge bauplanmäßig genau unter ihm, so daß es die Ausdehnung der Augen behinderte. Ohne ein Nützlichkeitsprinzip zur Erklärung heranziehen zu wollen, läßt sich doch ein Zusammenhang zwischen der Augenvergrößerung und dem Verlust des Transversum annehmen, so daß die Verschmelzung der lateralen Munddachlücke mit der Adductorlücke aus der Augenvergrößerung zu verstehen ist.

Unter accessorischen Gaumenlücken wollen wir solche verstehen, die sich, meist unregelmäßig auftretend, nicht aus dem typischen Lückenmuster des Reptilgaumens ableiten lassen. Dabei kann es sich um Durchbrechungen in einem einzelnen Knochenindividuum handeln, wie um die in den Gaumenfortsätzen der Maxillaria auftretenden, meist bindegewebig verschlossenen Öffnungen(*Rhea*), ebenso auch um Abspaltungen von einer anderen Gaumenlücke. So finden sich im System ganz ungleichmäßig verteilt Öffnungen, die vom Körper des Maxillare, dem Stiel des Processus palatinus des Maxillare und dem Palatinum umrahmt werden und rostral der Adductorlücke, aber lateral der Oberschnabellücke liegen (Abb. 4, 8); sie können keinesfalls der lateralen Gaumenlücke der Reptilien gleichgesetzt werden, da sie nicht durch das Transversum umschlossen werden. Wir finden sie bei den *Accipitres, Striges, Burhinus, Vanellus* u. a. Sowohl ihr Auftreten im System, wie ihr Verlust und ihre außerordentliche Variabilität zeigen, daß es sich um morphologisch völlig unwichtige Neubildungen handelt. Bei *Aegypius* (*Vultur*) findet man Stücke, die sie vollausgebildet oder bis auf einige Foramina verschlossen zeigen; u. a. fand sich ein Stück das sie links völlig geschlossen, rechts aber noch durch einige kleinere Öffnungen vertreten zeigte. Ähnliche Spalten finden sich bei manchen, hauptsächlich jüngeren und weiblichen Stücken von *Otis*. Sie liegen hier lateral der Oberschnabellücke und werden seitlich von Maxillare und Praemaxillare, medial aber vom Palatinum begrenzt.

Auf die bei dem Foetus von *Struthio* gefundenen accessorischen Lücken zwischen Processus palatinus maxillae, Processus palatinus praemaxillae und Vomer wurde schon hingewiesen.

IV. RÜCKBLICK.

Die Untersuchung bringt einen Vergleich zwischen Reptil- und Vogelgaumen mit dem Ziel die Veränderungen des Lückenmusters des letzteren morphologisch zu erklären.

Das Lückenmuster des Wirbeltiergaumens ist aus dem kinetischen Typus zu verstehen. Bei der Splanchnokinetik kann niemals eine den Gaumen quer unter-

teilende Spalte auftreten, weil das Parasphenoid von der Occipitalregion bis zur Ethmoidalregion als starrer Schädelkiel durchzieht, so daß gesonderte Hebungen der Ethmoidalregion nicht möglich sind. Beim typischen splanchnokinetischen Munddach finden sich immer paarige Längsspalten, niemals ein unpaarer Medianspalt oder Querspalten. Bei der Neurokinetik wird der Schädel in ein Maxillar- und Occipitalsegment geteilt, so daß ersteres gegen letzteres gehoben werden kann. Das setzt ein Scharnierspaltensystem voraus, das die beiden Segmente teilt und sich am Gaumen in Querspalten oder einem unpaaren Medianspalt äußert.

Nach VERSLUYS finden wir bei den Reptilien drei neurokinetische Typen die nach der Lage der Beugungszone unterschieden werden können: Meta-, Amphi- und Mesokinetik. Bei den Vögeln werden wieder zwei kinetische Typen gefunden, die in der Lage der Beugungszone voneinander unterscheidbar sind und auch von den Reptiltypen darin abweichen: Prokinetik und Rhynchokinetik. Die Beugungszone des Oberkiefers liegt bei ersterer inter- bei letzterer praeethmoidal.

Im Vergleich mit dem Reptilgaumen zeigt der der Vögel folgende Änderungen:

a) Wenn das Basipterygoidgelenk rückgebildet wird, verschmelzen Interpterygoidalspalt und Pteroccipitallücke. Das Diastema ist ein Teil des ersteren. Der rostral der spheno-pterygoidalen Gleitlagers liegende Teil des Interpterygoidalspaltes ist dem Diastema homolog, der caudal davon liegende dem Interpterygoidalspalt + Pteroccipitallücke (*Galli, Anseres*). Bei *Bubo* sind alle drei Lücken getrennt voneinander zu finden.

b) Die laterale Gaumenlücke der Reptilien verschmilzt bei den Vögeln durch Rückbildung des Transversum mit der Adductorlücke. Die Reduktion des Transversum und die Vergrößerung der Augen stehen vermutlich im wechselseitigen Zusammenhang.

c) Die Oberschnabellücke der Vögel entstand aus den primären Choanen der Reptilien und zeigt zwei in ihren Schicksalen verschiedene Abschnitte: Den rostralen Schnabel- und den caudalen Choanenabschnitt. Ersterer kann knöchern geschlossen werden, letzterer bleibt immer erhalten.

d) Mehrfach treten an verschiedenen Stellen des Munddaches accessorische Gaumenlücken auf, doch ist ihnen für den Vergleich mit dem Reptilschädel keine Bedeutung beizumessen.

Diese Umbildungen haben zu einer Verringerung der Zahl der Gaumenlücken geführt: Aus den beim Reptilschädel paarigen Choanen entsteht eine unpaare Oberschnabellücke, die laterale Gaumenlücke der Reptilien geht in der Adductorlücke auf und statt zweier, paariger an der Schädelbasis liegender Lücken findet sich jederseits nur eine. Zeigte der Reptilgaumen zehn bauplanmäßige Lücken, so besitzt der weitestveränderte Vogelgaumen nur fünf.

Bei *Steatornis* (*Caprimulgidae*), *Bucerotidae* und *Rhamphastidae* wurde eine

die beiden Palatina rostral und ventral der Choanengänge verbindende Knochenbrücke mehrfach beobachtet. Voraussetzung zu ihrer Bildung ist die unbewegliche Verbindung der beiden Palatina untereinander (Sympalatinie). So belanglos diese Knochenbrücke zu sein scheint, so ist sie doch das Analogen zum knöchernen Verschluß des Schnabelabschnittes der Oberschnabellücke im mittleren Gaumenbereiche. So wie der Oberschnabel nur dann ventral knöchern verschlossen werden kann (Desmognathie), wenn er nach dem Prinzip des starren Rahmens gebaut ist, so kann eine knöcherne Umfassung der Choanen nur bei sympalatinen Formen erfolgen, wenn also die Palatina keine gesonderten Bewegungen ausführen können. Diese beiden Prozesse stellen einen analogen Fall zur Bildung des sekundären knöchernen Gaumens bei Reptilien und Säugern dar. Solche sekundäre Knochengaumen können nur dann gebildet werden, wenn der Schädel akinetisch ist (*Crocodilia, Chelonia, Pseudosuchia* teilweise, *Theromorpha, Mammalia*). Da bei den Vögeln der Schädel nie akinetisch wird, müssen sich solche sekundäre knöcherne Gaumenbildungen auf Teile beschränken, wo eine Bewegung gegeneinander nicht stattfinden kann, also auf den Schnabelabschnitt bei Rahmenschnäbeln und auf den praechoanalen Palatinabschnitt bei sympalatinen Formen.

Das Lückenmuster der Palaeognathengaumen schließt sich an das der Neognathen weitgehend an, zeigt aber innerhalb der Gruppe starke Verschiedenheiten. Alle Palaeognathen sind rhynchokinetisch; *Casuarius* und *Apteryx* m. E. nur passiv. Die stärkste Kinetik zeigen *Struthio, Rhea* und die *Crypturi*. Das abweichende Gaumenbild von *Struthio* wird durch den Gaumen des Fötus an das der übrigen Palaeognathen angeschlossen. Damit ergibt sich, daß für alle Palaeognathen ein einheitlicher Ausgangstypus annehmbar wird, der dem Gaumentypus der *Crypturi* am nächsten kommt, was phylogenetisch und systematisch bedeutungsvoll ist.

LITERATURVERZEICHNIS.

Unter den gegebenen Verhältnissen war eine Durchsicht der gesamten einschlägigen Literatur nicht möglich. Hier werden nur die wichtigsten Arbeiten zitiert. Umfangreiche Schriftenverzeichnisse finden sich bei DE BEER, EDGEWORTH, LAKJER, LAMBRECHT, V. MARINELLI und VERSLUYS. Mit einem * bezeichnete Arbeiten waren mir nicht zugänglich.

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SOME REMARKS ON THE ONTOGENETICAL DEVELOPMENT OF THE SENSORY LINES ON THE CHEEK IN FISHES AND AMPHIBIANS

BY

NILS HOLMGREN and TORSTEN PEHRSON

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INTRODUCTION.

The homologisation of the different parts of the sensory line system in fossil fishes largely must depend upon a thorough knowledge of this system in living fishes, where such a knowledge can be obtained by means of anatomical and embryological investigations. Anatomical knowledge only is not sufficient even for homologisation of the different parts of this system in recent fish types

but must be supplemented by embryological researches, which often explain anatomical facts, else obscure. Especially, when the problems of the sensory lines on the cheek are concerned, anatomical conditions alone can not afford such facts which are necessary for an explanation, as all cheek lines are innervated from a common source: the lateralis components of the hyomandibular nerve. Here embryological evidence must be guiding. This also, was perceived long ago when for instance ALLIS (1934) made his well-known study of the morphology of the lateral sensory line system on the head of fish and *Necturus*. He based his embryological argumentation on the conditions in *Necturus* according to the investigation of Miss PLATT (1896), and upon the representation of the cheek lines of an embryo of *Ceratodus*, as published by GREIL (1913). HOLMGREN in his "General morphology of the lateral sensory line system of the head in fish" used the ontogenetical method only for explaining the conditions in rays. In his extensive study of "The sensory lines and dermal bones of the cheek in fishes and amphibians" STENSIÖ (1947) has collected all the ontogenetical material, hithertoo available, for establishing a general pattern of the sensory lines of the cheek. According to this pattern there are the following lines present on the cheek: 1) an infraorbital line with its postorbital and suborbital parts, 2) a preopercular line, 3) a mandibular line, 4) a supramaxillary line ("horizontal pit-line"), 5) a postmaxillary line ("vertical pit-line") and 6) an oral line. The absence of any jugal line and the new terminology for the horizontal and vertical pit-lines, respectively, strike as the new points in this enumeration. The jugal line is according to the new conception the preopercular line of which the dorsal portion has got a connection with the infraorbital line in front of and below the spiracle instead of joining the temporal part of the main lateral line behind the spiracle.

The new theory seems to be based to some extent upon the embryological evidence gathered from the literature. This literature is very scarce, at least concerning the early development of the sensory lines, and is not very reliable. Exceptions are for instance PLATT's paper on *Necturus* and the papers of STONE (1922) on *Ablystoma* and KNOUFF (1935) on *Rana*.

In the present paper we will undertake a revision of our knowledge of the ontogenetical development of the cheek-lines, beginning with the conditions in the shark, *Squalus acanthias*.

SENSORY CHEEK LINES IN SQUALUS ACANTHIAS.

In 1940 HOLMGREN published a few pictures of the developing sensory lines on the cheek of *Squalus*. At that time his interest was concentrated upon the question of the development of the endocranium. Therefore insufficient

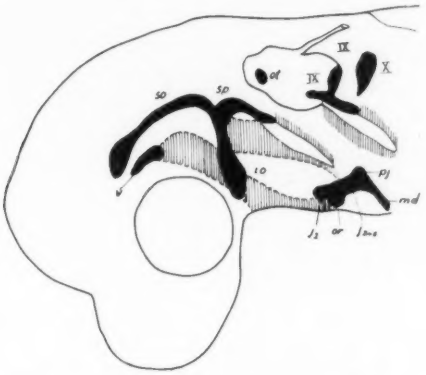

Fig. 1. *Squalus acanthias.* Embryo 18 mm. Original reconstruction.

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attention was paid to the development of the sensory lines. Now he has redrawn his reconstructions and made new ones, where necessary.

In the 16.5 mm stage the lines on the cheek are represented by a bent rod of thickened epithelium, of which the anterior, horizontal, limb represents the jugal line whereas the down-bent posterior portion is the primordium of the mandibular line. The angle in which these two portions of the line meet, lies immediately ventral to the lower end of the spiracular gill cleft. The distance between the anterior end of the jugal line and the infraorbital line is wide.

In a 18 mm embryo (fig. 1) the picture has altered in the following way. On the lower side of the jugal line, slightly anterior to its middle, a line has developed, extending on the mandible in front of the mandibular line. This new line component is the oral line. The angle where the jugal and the mandibular lines meet is marked by a small dorsal outgrowth (*pj*), lying in the prolongation of the jugal line ventral to the spiracular cleft. In this stage as in the preceding the primordia of the components of the cheek system form a complete continuum. The distance between the jugal line and the infraorbital line has decreased, but is always rather wide.

The distal end of the oral line as well as that of the mandibular merge with the thick epithelium of the border of the mouth where the two lines, thus, may be considered as joined.

In a 22 mm embryo (fig. 2) the cheek-line system is principally the same as in the preceeding stage, but that part of the jugal line lying behind the oral line has curved dorsad, so that a sharp angle has formed between the anterior and the posterior parts of the jugal line. There are also signs indicating a loosening of the continuity between these parts of the jugal line. The dorsal outgrowth from the posterior end of the jugal line or the upper of the mandibular is also present in this stage. The distance between the anterior end of the

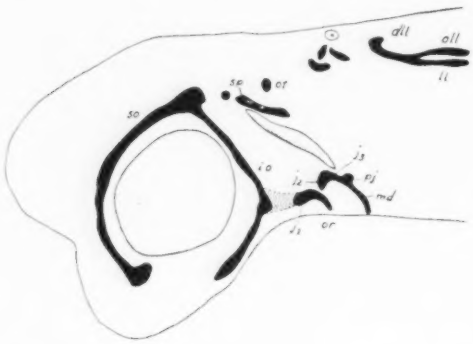

Fig. 2. *Squalus acanthias.* Embryo 22 mm. Original reconstruction.

jugal line and the infraorbital line has diminished still more and a band of the epithelium between these lines is thickened.

In the 24.5 mm stage (fig. 3) the essential changes of the cheek-lines consist in continued curving dorsad of the posterior portion of the jugal line connected with a subsequent lengthening of the mandibular line. The curving of the line takes place decidedly in front of the spiracular cleft which is closing up from below, leaving a quite visible scar or seam just behind the upbent jugo-mandibular line. The anterior part of the jugal line has become detached from the posterior part of the same, but on the point of separation there has been left a pad of thickened epithelium connected with the anterior part. This pad marks the point where the oral line issues from the jugal. The outgrowth at the dorsal end of the mandibular line lies as before at the lower end of the spiracle. The connection between the infraorbital line and the anterior end of the jugal line is very conspicuous but does not develop into a real line in *Squalus*.

At the 27 mm stage (fig. 4) the future pattern of the cheek-lines is quite descernable. This stage seems to be somewhat variable. Some specimens are as the preceding one, with the difference that the knob-like outgrowth at the lower end of the spiracle has disappeared altogether, that the posterior portion of the jugal line has curved up more, in front of the still closing spiracular cleft and that the pad of thickened epithelium at the junction point between the anterior and the posterior parts of the jugal line has developed into a short upbent posterior portion at the posterior end of the anterior part of the jugal line. In other specimens the anterior limb of the posterior part of the jugal line is completely detached from the anterior part and now forms a downbent hook in front of the lower end of the spiracle. In later stages this hook becomes less pronounced forming a short frontally directed portion of the line. The oral line is detached from the rest of the cheek system.

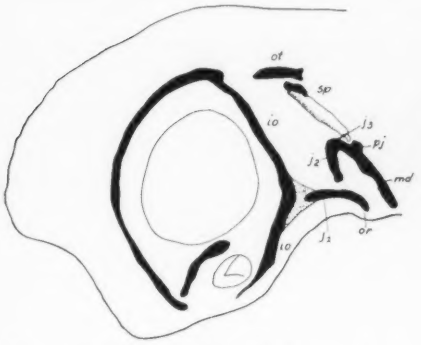

Fig. 3. *Squalus acanthias.* Embryo 24.5 mm. Original recontruction.

Fig. 4. *Squalus acanthias.* Embryo 27 mm. Photographical representation.

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This additional investigation upon the ontogeny of the cheek-line system in *Squalus* seems to give full evidences for the following conclusions.

1) HOLMGREN's earlier assumption that the knob at the dorsal end of the mandibular line is the rudiment of a preopercular line is incorrect. It is not the rudiment of any preopercular line and does not grow upward behind the spiracular cleft as presumed by STENSIÖ.

2) There is no differentiated preopercular line present in *Squalus.*

3) What was considered earlier to be a preopercular line in sharks is a posterior portion of the jugal line and the dorsal portion (the prospective preopercular line) of the mandibular line taken together.

4) The knob at the upper end of the mandibular line in early stages probably represents the canal branch, found by ALLIS on the posterior border of the so called preopercular canal in *Chlamydoselachus* (fig. 5).

5) The pad of thickened epithelium at the posterior end of the anterior part of the jugal line forms (probably) the upbent portion of this cheek-line in *Squalus, Etmopterus, Mustelus* and others and the backward continuation of the "jugal" canal in *Chlamydoselachus.*

6) The thickened epithelium connecting the jugal line with the infraorbital represents the anterior part of the "jugal" canal in *Chlamydoselachus.*

7) The "middle cheek-line", which HOLMGREN described in *Chlamydoselachus* 1942 is the downbent anterior portion of the posterior part of the jugal line.

8) The jugal line of Sharks, thus, is a very broken line consisting of an anterior horizontal portion: jugal 1 (j_1), a "middle cheek line" jugal 2 (j_2) and a posterior part, jugal 3 (j_3). This system of line components has been interpreted (STENSIÖ 1947), as a system of supramaxillary lines ("horizontal pit-line") and the "preopercular line".

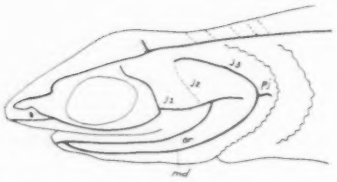

Fig. 5. *Chlamydoselachus anguineus.* Embryo 127 mm.

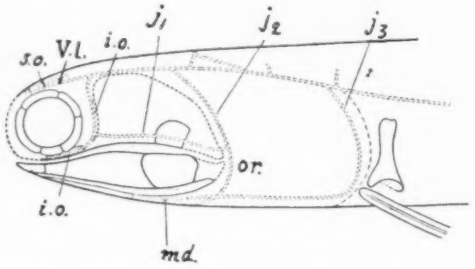

Fig. 6. *Acanthodes.* Head, according to WATSON (1937).

9) The error committed concerning the development of the cheek-lines in sharks is HOLMGREN's, as he was impressed by earlier workers to believe in the presence of a preopercular line and therefore did not investigate the development further than to the 24.5 mm stage in *Squalus.*

SENSORY CHEEK LINES IN ACANTHODIANS.

In 1942 HOLMGREN tried to give an interpretation of the cheek line system in Acanthodians, comparing them with sharks, especially *Chlamydoselachus.* At that time he believed in a postspiracular preopercular canal in the sharks. There could thus, scarcely be any other prespiracular line present in the space between the "jugal" line and the cephalic part of the lateral line, than the "middle cheek line". At present, as it has become clear that the "preopercular line" in sharks is prespiracular and belongs to the jugal line system, the cheek line system of the lower *Acanthodians* must be interpreted in a somewhat different way than earlier.

The basis of an interpretation, now, as in 1942, is the reconstructions of WATSON which still are the only available. As HOLMGREN in 1942, we begin with *Acanthodes* (fig. 6). In this fish HOLMGREN considered the cheek lines to be a longitudinal jugal line, meeting the transversal "middle cheek line" at the mouth angle and another transversal, the "preopercular", at the posterior border of the gill cover. Both the transversal lines reach the cephalic part of the lateral line. The posterior of these lines, ventrally, bends sharply frontad and continues on the lower jaw. An oral line is connected with the hindmost end of the "jugal line", where it also meets the "middle cheek line".

Contrary to this interpretation STENSIÖ (1947) considers the "middle cheek line" to be a preopercular line and the "preopercular" line of HOLMGREN's description to be a scapular line. "That HOLMGREN's 'preopercular' line can

not be a real preopercular line is clear without comment" (STENSIÖ 1947, p. 48). But is it really so clear? "Because of its position far caudally and its connection with the main lateral line, the line here in question (*Scc*) must be assumed to have been supplied by lateralis branches from the nervus vagus." To this assumption we must remark that the line lies upon a gill cover which is said by STENSIÖ to be a hyoid gill cover, thus belonging to a cephalic region which always is innervated by the hyomandibularis nerve. Its connection with the main lateral line is no reason for considering it to be innervated by vagus branches. Its point of departure from the lateral line lies in front of a transversal dorsal line, which, considering its position, well may answer to the supratemporal commissure as described and figured in *Ischnacanthus* and *Diplacanthus*. The point at which it meets the cephalic portion of the main lateral line is, thus, about where the preopercular line meets it in fishes where a real preopercular line exists. STENSIÖ has considered the "preopercular" line in *Acanthodes* a "scapular" line (vagus-innervation) and interpreted its connection with the mandibular line as a part of the ventral lateral line, an interpretation that should be reasonable if its innervation had been stated to be vagal. WATSON's interpretation of this line as an opercular line is more reasonable, but then its connection with the mandibular line is not explained.

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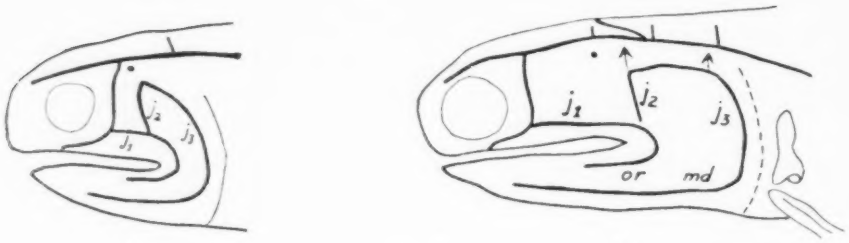
The statement that there is no preopercular line present at all in sharks makes it necessary to revide our conception of the cheek line system in the Acanthodians. In *Acanthodes* it is somewhat difficult to locate the spiracle. It must, however, have been situated somewhere between the mandibular and the hyoid arches, thus, far in front of the posterior border of the gill cover. This point was, probably, situated in front of the foremost transversal cheek line, in the pictures labelled j_2, thus, in front of the middle cheek line and the "preopercular" line in HOLMGREN's description (1942). In sharks these lines are clearly prespiracular. The homologisation of the lines in sharks and *Acanthodes* may therefore at first sight seem irrational. The following considerations may, however, explain the possibility of homologising the "middle cheek line" with the jugal 2 and the "preopercular" line with jugal 3 in sharks. In comparison with other Acanthodians the head of *Acanthodes* must be described as excessively lengthened. It is therefore to be assumed that it was, ontogenetically, much shorter. At early ontogenetical stages the cheek lines were, probably, located far frontally. If they were arranged according to the shark type they had been situated as in the fig. 7 A with the jugal 2 and 3 meeting below the spiracle or perhaps in front of it as in *Euthacanthus* (fig. 8) where the upper end of jugal 3 lies far in front of the spiracle. When the prolongation of the head took place, the jugal 2 and 3 could move caudad below the spiracle and became postspiracular (as in *Mustelus*) as shown in fig. 7 B. If the jugal 2 and 3 respectively extended dorsad and joined the



A B

Figs. 7 A—B. Hypothetical stages of the development of the sensory lines in *Acanthodes*.

cephalic part of the main lateral line the *Acanthodes* conditions would be attained.

If the joined middle cheek line and the third portion of the jugal line in *Chlamydoselachus* (fig. 5) connected with the main lateral line dorsally the *Acanthodes* condition should arise. This is a construction, but a construction without which the cheek line system of *Acanthodes* must remain unexplained. Yet, these constructions are considerably less far fetched than those attempted in a comparison with Arthrodires, Holocephalians, Crossopterygians, Holosteans, Teleosts and Amphibians (cf. STENSIÖ, p. 49).

Also the other Acanthodians, of wich the cheek lines are tolerably well known, are explained by the conditions in sharks. In *Euthacanthus* HOLMGREN (1942) has suggested a jugal line and a "middle cheek line", whereas STENSIÖ (1947) has assumed the presence of a supramaxillary line: first portion (hc_1 = HOLMGREN's jugal line) and a preopercular line. To them he has added a quite hypothetical second portion of the supramaxillary line (hc_2), which he has drawn arbitrarily between the hc_1 and the "preopercular line". *Ischnacanthus* belongs to the *Euthacanthus* type. A special type is *Diplacanthus* with small mouth, where only a short first portion of the "supramaxillary line" connected with the oral line is known. There is no "preopercular" line found in the fossils.

About the different Acanthodian types STENSIÖ says: "None of these types has any particular resemblance to the type of cheek lines in sharks, and the researches here carried out have thus in this respect led to an opinion different from that put forward by HOLMGREN (1942 a, p. 26). On the other hand it is evident that the preopercular line in the *Euthacanthus* type reminds one much of the preopercular line in the Crossopterygians and Amphibians, and that the posterior connection of the oral line with the mandibular line in the *Euthacanthus* and *Acanthodes* types is also a Crossopterygian-Amphibian like character. The preopercular line in the Acanthodes type is suggestive of the corresponding line in *Arthrodira* and higher Actinopterygians."

We do not agree with these interpretations of STENSIÖ. In the preceding

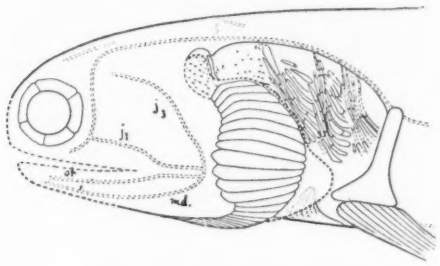


Fig. 8. *Euthacanthus*. Head, according to WATSON (1937).

lines we have given evidences for the *Acanthodes* type being a perfectly selachian type, nearly resembling that of *Chlamydoselachus*. The *Euthacanthus* type (fig. 8) is also nearly a perfect selachian type. This is perfectly clear when comparing it for instance with *Mustelus*, where the middle cheek line is reduced. This interpretation involves that we have altered HOLMGREN'S standpoint (1942) as to the nature of the "middle cheek" line in *Euthacanthus*, this line being the third portion of the jugal line and the second (the real "middle cheek" line) being absent. The only difference between the *Mustelus* type and the *Euthacanthus* type seems to be that in the latter the oral and mandibular lines meet caudally. But in *Ischnacanthus* they are separate (as far as the reconstruction shows).[1]

The difference in our standpoints depends upon the different interpretation of the "preopercular" line in sharks, where STENSIÖ believed that the "preopercular" line grows up caudally to the spiracle, whereas it was shown in the present paper that the "preopercular" line is no such line at all but a third division of the jugal line, a special supramaxillary line not existing.

That the "preopercular" line in Acanthodians should be suggestive of the "preopercular" line in *Arthrodira* and higher Actinopterygians is not sufficiently based upon facts. 1:0 The "preopercular line" in *Arthrodira* and higher Actinopterygians is postspiracular, in *Euthacanthus* prespiracular. 2:0 The "preopercular" line in Arthrodirans is certainly no preopercular line (see p. 299) at all.

We may end this discussion of the sensory lines on the cheek in Acanthodians with the following statements.

1. There is no preopercular line in Acanthodians.

2. What has earlier been called the preopercular line is the third portion of the jugal line.

[1] HOLMGREN'S opinion (1942) also seems reasonable, but involves the assumption that the third portion of the jugal line has disappeared and that its mandibular continuation has shifted to become a mandibular continuation of the "middle cheek line". These assumptions seems us now to be too speculative to be accepted, the more so as an immediate comparison with *Mustelus* is possible.

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3. The "middle cheek" line or second portion of the jugal line is only present in *Acanthodes* (HOLMGREN 1942).

4. What HOLMGREN called the "middle cheek" line in the older Acanthodians (1942) is the third portion of the jugal line.

5. What has been called by HOLMGREN (1942) the jugal line is the first portion of the jugal line.

6. What STENSIÖ called the first portion (hc_1) of the supramaxillary line is the first portion of the jugal line.

7. There are at least two types of Acanthodians as far as the cheek lines are concerned: an older type (*Euthacanthus*) where these lines readily are as in Mustelid sharks, and another, younger (*Acanthodes*), where the lines are possible to compare with those in *Chlamydoselachus*. Both these types must be derived from a common selachian type with a differentiated jugal line.

8. Thus the Acanthodians are decidedly sharklike as to their cheek lines.

The absence of a real preopercular line (behind the spiracle) annihilates STENSIÖ's argumentation against WATSON's theory of the fullsized mandibular gill slit in Acanthodians. STENSIÖ says: "If a fullsized mandibular (spiracular) gill opening persists in Acanthodians as WATSON believed, this gill opening, according to what has been set forth above, must lie in front of the preopercular line, but, as is well known from WATSON's own researches, the Acanthodians have no gill opening situated so far anteriorly. WATSON therefore locates the full-sized mandibular (spiracular) gill opening of the Acanthodians medially to the principal gill-cover (*Op.hy.*, fig. 11 A). That it cannot possibly have had this position, however, is evident beyond question, for it would then have been crossed by the nerves for the preopercular, supramaxillary and postmaxillary lines. A fullsized mandibular gill-opening cannot of course, be crossed by freely running nerves. Hence there is no full-sized mandibular gill-opening in *Acanthodians* but the mandibular gill-opening in them had been reduced and modified into a spiracle, quite as is the case in other groups of primitive fishes".

All the arguments upon which STENSIÖ has based this conclusion are jeopardized by the simple fact that there is no preopercular line in sharks and probably also not in Acanthodians and that what STENSIÖ believed to be a preopercular line in sharks is clearly prespiracular. On other grounds HOLMGREN (1942) had, however, come to the conclusion that the full-sized gill-opening in Acanthodians is very doubtful. But we will not go so far in our conclusions as to suggest that the principal gill-cover in *Euthacanthus* was a hyoid gill-cover and the small flap at the anterior border of the spiracle a mandibular.

SENSORY CHEEK LINES IN DIPNOI.

The embryonic sensory line system on the cheek of *Neoceratodus* has been depicted by GREIL (fig. 16). His picture is wrong throughout, as PEHRSON has demonstrated in a newly published paper (1949). Unfortunately GREIL's picture has been used by ALLIS and STESIÖ as an important basis for their deductions. Especially the circumstance that GREIL has figured a non existing preopercular line in *Neoceratodus* has caused some trouble.

PEHRSON has described and figured a series of developmental stages of *Neoceratodus*. It consists of reconstructions of the sensory line system in 8.6, 10, 10.6, 11.5, 12, 12.6, 14.5, 16.5 and 43.5 mm stages. This series leads with small interruptions to the young fish, of which HOLMGREN (1942) has described the lateral line system on the cheek. There is thus no need of interpolating any hypothetical stages (STENSIÖ 1947, figs. 8 and 9). It must, however, be remarked that there is a certain variability present, so that the right and left sides of the embryo do not behave quite correspondingly in all details. This is an advantage, which has enabled PEHRSON to fill in certain smaller gaps in the morphological series.

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PEHRSON's essential results are as follows:

In the stages 8.6—11.5 mm the sensory lines are represented by placodes, in the 12 mm stage the placodes are breaking up in neuromasts generally forming defined lines.

In the 8.6 mm stage (fig. 9) the placodes on the cheek form a V with the angle pointing upwards. In the 10 mm (fig. 10) stage the posterior limb of the inverted V has curved caudad, so that the distance between the limbs has widened. On the anterior border of the anterior limb a short branch is seen. This branch, later, will join the infraorbital line. On the posterior border of the posterior limb a small knob has arisen. This knob represents the first appearing primordium of the opercular neuromast system. This system, however, disappears later. Already at this early stage it is possible to recognise the chief portions of the cheek system. The anterior short branch is the jugal 1 (j_1) section of the jugal line, the raised up portion of the anterior limb is the jugal 2 (j_2) and the posterior limb down to the opercular primordium represents the jugal 3 portion (j_3), as will be explained below. From the jugal 1 portion issues the oral line, and from the jugal 3 the preoperculo-mandibular line. Already at the 10 mm stage a solitary, independent placode (in PEHRSON 1949, labelled *y*) is found between the upper end of the jugal system and the infraorbital placode. This placode either may join the infraorbital line (fig. 11), or the jugal 3, or remain separate (fig. 10). It will be named the *secondary jugal line* placode (*js*).

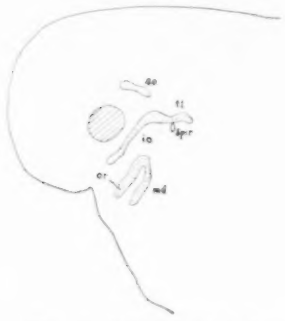

Fig. 9. *Neoceratodus forsteri.* Embryo 8.6 mm. According to PEHRSON.

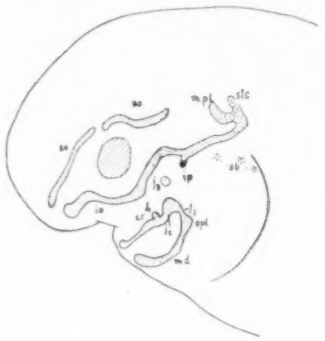

Fig. 10. *Neoceratodus forsteri.* Embryo 10 mm. According to PEHRSON.

At the 10 mm stage a short spiracular line joining the main lateral line is present. The spiracular organ is the first neuromast in a series of four suprabranchial neuromasts. At the 11.5 mm stage (fig. 13) the spiracular placode is distinctly enlarged (*sb*) and budding out a series of neuromasts of which the hindmost, at the 12 mm stage, apparently, joins the main lateral line level with the supratemporal commissure. These neuromasts later disappear. PEHRSON (1949) has demonstrated that this line is continued caudad by three neuromasts at the upper end of the branchial arches (the suprabranchial neuromasts). Also these neuromasts later disappear.

The 10.6 mm stage (fig. 12) very much resembles the 10 mm stage but at the posterior border of the jugo-mandibular line portion a primordium of a ventral line (*vl*) is seen somewhat below the primordium of the opercular series. This primordium seems to bud off the posterior gular line.

The 11.5 mm stage (fig. 13) is very important for the understanding of the cheek line system in *Neoceratodus*. In this stage the jugo-mandibular line has bent further caudad and the anterior limb of the original inverted V has differentiated into a lower portion, the oral line, and an upper portion (the jugal 2), the fate of which will be tolerably clear from the older stages of the series. This upper portion is strongly bent caudad as to become dorsally nearly parallel to the upper end of the jugo-mandibular line. Its lower part then runs frontad, towards the upper end of the oral line.

The lower horizontal part of the jugal 2 line is about to desintegrate, breaking up in smaller units, the fate of which can be traced in the 12 mm stage (fig. 14) where two pit lines have been organized from the lower portion of the jugal 2. These pit lines are, the anterior: the secondary mandibular line (*smd*)[1] and the posterior: the secondary oral line (*sor*). The upper

[1] This name is not very appropriate as it seems to involve that this pit-line has something to do with the mandibular line what it has not, as far as we know.

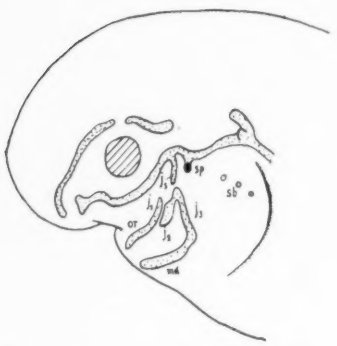

Fig. 11. *Neoceratodus forsteri.* Embryo 10 mm. According to PEHRSON.

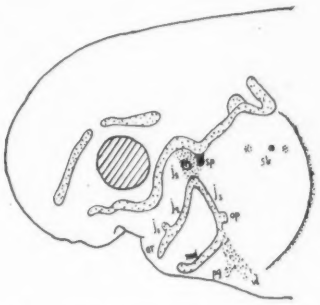

Fig. 12. *Neoceratodus forsteri.* Embryo 10,6 mm. According to PEHRSON.

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Fig. 13. *Neoceratodus forsteri.* Embryo 11.5 mm. According to PEHRSON.

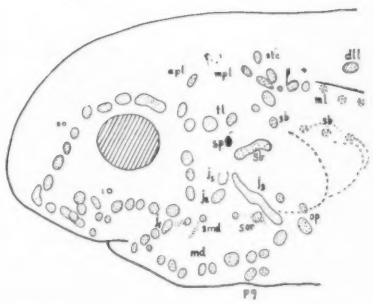

Fig. 14. *Neoceratodus forsteri.* Embryo 12 mm. According to PEHRSON.

portion of the jugal line remains as the jugal 2 proper which in *Neoceratodus* also is developed as a pit line. The three pit lines of the embryo are the primordia of the three pit-lines on the cheek (fig. 15), figured in HOLMGREN—STENSIÖ (1936, p. 378) and by HOLMGREN (1942). The three of them thus result from the upper part of the anterior limb of the inverted V in younger stages. During the further development the jugo-mandibular line joins the postorbital part of the infraorbital line. This junction takes place by means of the separate placode (*js*), described and figured by PEHRSON as the *y*-placode in the 10 mm stage named here the *secondary jugal placode*. The development of all these cheeklines takes place in a space of the cheek lying distinctly in front of and below the locus of the spiracle. The oral and mandibular lines are already at the 10 mm stage diffusely joined apically. This junction is very conspicuous at the 11.5 mm stage and at all stages beyond.

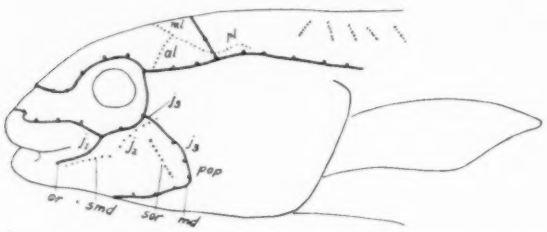

Fig. 15. *Neoceratodus forsteri.* Young fish, 2 1/4 years old, according to HOLMGREN (1942).

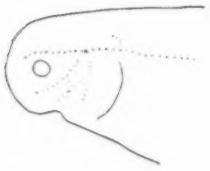

Fig. 16. Sensory lines on head of Neoceratodus, according to GREIL.

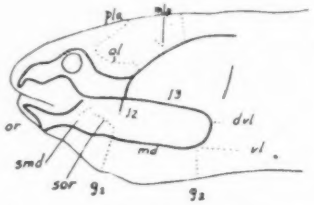

Fig. 17. *Protopterus annectens.* Larval specimen, according to HOLMGREN (1942).

Excepting some minor details the cheek system of *Protopterus* (fig. 17) develops as that of *Neoceratodus* and will not be treated here. It may, however, be pointed out that the jugo-mandibular line joins the infraorbital earlier than the oral line, and that no unquestionable special secondary jugal placode has been found. That fact may depend thereupon that this placode is included in the frontal end of the jugal 3 line, where a short placode section establishes the junction with the infraorbital line.

How now to explain the conditions in the larval *Neoceratodus?* PEHRSON has pointed out certain agreements between the Dipnoans (and *Selachians*) and *Necturus*. With both these the Dipnoans share certain characters and both could rather well serve for comparison. ALLIS and STENSIÖ have used *Necturus* owing to this amphibian being the most reliably investigated of the urodele amphibians. We, however, prefer to begin with a comparison with Selachians (*Squalus*), as this fish represents a more primitive vertebrate type than the amphibians.

Accepting the *possibility* of an explanation of the dipnoan conditions by means of those in *Squalus*, an explanation is rather simple using the 11.5 mm stage of *Neoceratodus* comparing it with the 24.5 mm (and older stages) stage of *Squalus*. There are differences, of course, of which the most striking is produced by the more terminal position of the lower jaw in the Dipnoan, which has caused that the oral and mandibular lines extend more or less horizontally frontad, whereas they are directed ventrad or ventrocaudad in the

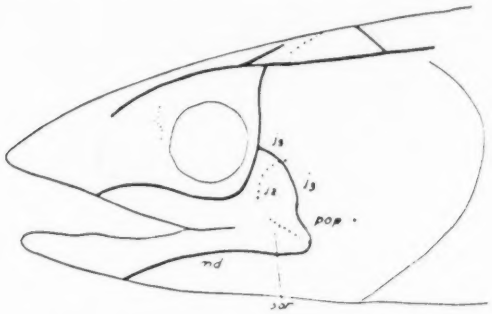

Fig. 18. *Dipterus valensiennensi.* Essentially according to GRAHAM-SMITH and WESTOLL (1937).

Squalus embryo. Otherwise the agreement is very striking. In *Neoceratodus* there is the same dorsal bend of the posterior portion of the jugal line as in *Squalus*. The anterior limb of this upbent portion of the jugal line in *Squalus* corresponds to the dorsal part of the anterior limb of the "inverted" V in earlier stages, which is desintegrating in the 12 mm stage. If this comparison is correct the desintegrating line portion corresponds to the "middle cheek line" in *Chlamydoselachus*, disappearing in other sharks. In the Dipnoans the "middle cheek line" instead of disappearing gives rise to the three "supernumerary" lines in these fishes.[1] Next step in the transformation of the shark pattern is effected when the primary oral line joins the infraorbital and, then, when the jugo-mandibular line by means of the secondary jugal (*js*) placode joins the postorbital portion of the infraorbital line. This latter connection is a new one, the secondary jugal line (*js*), not existing in the sharks. We will point out the presence in *Neoceratodus* of the postjugal opercular placode (or placodes), which very much reminds of the knob on the jugo-mandibular line in *Squalus* and the postjugal canal branch in *Chlamydoselachus*. This point marks the posterior end of the jugal line. Below it the mandibular line begins with a posterior (upper) section which may be considered to be the primordium of a primary preopercular line and which extends ventrad to the point where the ventral lateral line issues from the posterior end of the mandibular line.

[1] The dorsal of these lines, apparently, is what is left of the second section (j_2) of the jugal line after the two others have split off. The anterior of these lines HOLMGREN (1942) termed the primary mandibular line, and the posterior was named the secondary oral line. This terminology was suggested by the conditions in the Pteraspids where the ventral longitudinal lines are joined closely together with the infraorbital line. In 1942 HOLMGREN believed that the two oral lines in Dipnoans corresponded to these two lines in Pteraspids. If that had been the case the two posterior lines in the *Dipnoi* had been a secondary oral and a secondary mandibular line. A comparison, however, with lowly organised Gnathostomians seems to make it clear that the secondary lines are developed between the two primary lines. Thus, the terminology should be altered in the following way: Primary oral line = primary oral line, primary mandibular line = secondary mandibular line, secondary oral line = secondary oral line, secondary mandibular line = primary mandibular line.

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In the palaeozoic *Dipterus valenciennesi* (fig. 18) which has been restored by GRAHAM-SMITH and WESTOLL (1937), the cheek lines are much as in *Ceratodus* but with the difference that the first portion of the jugal line (j_1) with the primary oral line is missing and the second portion (j_2) is developed as a strong pit-line. The secondary jugal line (*js*) is longer than in *Neoceratodus*. The limit between the jugal line and the preoperculo-mandibular is not possible to determine but ought to lie rather low on the cheek. The jugo-preoperculo-mandibular canal runs as in the adult *Neoceratodus* through a series of small bones of which the lower ones may represent a preopercular series, the higher up located a squamosal. A complete preopercular line consisting of a ventral and a dorsal (postspiracular) portion, thus, is not present.

On the quadratojugal part of the *Dipterus* skull is a rather long frontally directed pit-line, which tends to join the jugal 2 line. This pit-line has been called by STENSIÖ the postmaxillary line or proximal part of the oral line. The only reliable way of coming to an understanding of this line is to resort to the conditions in living lungfishes, and there *Neoceratodus* delivers a good assistance. There are, as HOLMGREN already has described (1942), three pit-lines in the space between the oral and jugo-mandibular lines. Of these the dorsal one is the second portion of the jugal line (j_2), the anterior a secondary mandibular line (called 1942 and by PEHRSON a primary mandibular line) and the posterior the secondary oral line. A comparison between *Dipterus* and *Neoceratodus*, based upon the really ascertained evidences, must result in the interpretation of the questionable pit-line as answering to the posterior of the pit-lines in *Neoceratodus*, called by HOLMGREN the secondary oral line. The only difference between the two lines is that the latter is more vertical and free in *Neoceratodus*, more horizontal and joined with the jugo-mandibular line in *Dipterus*. There is no evidence for assuming that the primary oral line is present in *Dipterus* and even less evidence that the quadratojugal line in *Dipterus* should represent a postmaxillary part of a primary oral line.

This conclusion is very strongly supported by the conditions in *Protopterus*. PEHRSON has shown that the three pitlines of *Protopterus* develop just as in *Neoceratodus*, a dorsal representing the remainders of the second section of the jugal line, the two others deriving from the placode of this line portion. The posterior of these two lines, which HOLMRGEN has previously (1942) named the secondary oral line, always becomes joined with the mandibular line, as the quadratojugal pitline in *Dipterus*. In some specimens (HOLMGREN 1942), this line also is connected with the pitline which represents the second portion of the jugal line, from which it is derived (PEHRSON). The conclusion, derived from these evidences, is that the posterior of the dipnoan pitlines belongs to a so called "vertical pitline", but *not* to a primary but to a *secondary oral line*, as the primary line is simultaneously present in recent Dipnoans. This

conclusion opens up a completely new way to an understanding of the "vertical pitline" in teleostomian fishes, as will be stated later on in this paper. At this place we may satisfy ourselves with the statement that *Dipterus* has the secondary oral and the (primary) mandibular lines, just as the osteolepiform Crossopterygians.

SENSORY CHEEK LINES IN URODELA.

We, now, turn our attention to *Necturus* where the development of the cheek lines has been admirably investigated by Miss PLATT. To make sure that there is no mistake in PLATT's description we have made some reconstructions of embryos at the same stages as investigated by PLATT. Her results are correct, except in two minor points. The primordia of the mandibular and oral lines are connected with each other, apically, already in the 12 mm stage (fig. 20), and at the 12 mm stage the cheek system is connected with the postorbital line by means of thickened epithelium. This connection lies below and in front of the locus of the spiracle. At the 15 mm stage (fig. 20) the connection between the tips of the oral and mandibular lines is retained.

PEHRSON has pointed out that there is a great general agreement between the 15 mm stage of *Necturus* and the 12 mm stage of *Neoceratodus,* an agreement that can not be explained as occasional. In young specimens (10—12 mm) there is the inverted V-stage (fig. 19) with the two limbs connected ventrally by thickened epithelium. The anterior limb of the V partly represents the oral, the posterior the jugo-mandibular line. The pointed, prolonged angle of the V represents the main part of the primary jugal line. This stage may also be compared with the 18 mm stage of *Squalus* (fig. 1). Also in *Neoceratodus* such a somewhat prolonged angle is present. In the 15 mm *Necturus* (fig. 20) this angle has split up longitudinally into two parallel lines, which, ventrally, are figured as continuous with the oral and the mandibular lines respectively.[1] In *Neoceratodus,* at the 11.5 mm stage, (fig. 13) the part of the jugal line which is curved dorsad presents, also, an apical part where the two limbs of the bent line are nearly parallel. In *Necturus* the two limbs of the primordial inverted V separate, the posterior bending caudad, the anterior frontad. At the angle of the mouth the anterior limb has an outgrowth which ultimately gets "connected" with the infraorbital line. The upper end of the system also "joins" the infraorbital line (postorbital part). In *Neoceratodus* the posterior limb of the V, only, joins the postorbital line by means of a special placode, whereas the anterior limb partly desintegrates, so forming the three pit-lines on the cheek.

[1] In our reconstructions of the 15 mm stage we missed this continuity partly. In *Hynobius* this continuity also is doubtful.

According to this explanation the jugal line of *Necturus* consists of the same three components as that of *Squalus* and Dipnoans, viz. a short, anterior part, the jugal 1 line, "connected" with the infraorbital line, a long strongly dorsad curved portion of which the anterior limb corresponds to the "middle cheek line" (jugal 2), and a posterior limb, corresponding to the posterior portion, jugal 3, of the jugal line in sharks and Dipnoans (the "preopercular line" of earlier writers). An ordinary secondary jugal line is not developed. As the middle and the hind portion both "join" the postorbital line there are three connections between the infraorbital system and the lower jaw. Two of them (j_1 and j_2) are connected with the oral line and one with the mandibular (j_3).[1]

Before leaving the Urodeles we wish to point out some peculiarities concerning some other features of the sensory line system in *Necturus* and other Urodeles, which may be of some importance in comparison with other vertebrates.

In a 12 mm *Necturus* (fig. 19) the supraorbital line placode is a short, broad longitudinal band dorsal to the posterior half of the eye, and the infraorbital line a band running in a ventral direction to the posterior border of the nasal placode. From the angle, where the supraorbital and the infraorbital placodes meet, the "otic" placode (*sp*) is about to be detached from the orbital placodes. It is located between the posterior end of the supraorbital placode and the spiracle, near both. On the posterior end of the supraorbital placode there is a weak, broad, dorsal process present (fig. 19, *xx*). The glossopharyngeal placode is situated very far from the "otic".

In a 15 mm embryo the supraorbital line has grown apically, frontally to the eye, and down in front of the nasal sac. The infraorbital line, also, is much longer than before. Both lines now are directed more or less vertically (for details see fig. 20). At the posterior end of the supraorbital line a strong frontally directed process (*al(xx)*) has developed from the little process in the 12 mm stage. This process is the primordium of the medial row of neuromasts, typical of many Urodeles. This inner row, thus, has not arisen through doubling of the original placode, but, is a special, comparatively independent structure, that may be interpreted as a frontally directed anterior pit-line comparable with the anteriorly directed anterior pit-line in *Protopterus* (fig. 17). The "otic" placode now is completely detached from the orbital system. It is innervated by a short nerve fibre issuing from the lateralis ganglion (fig. 20). The distance between the "otic" placode and the glossopharyngeal-vagal placodes is longer than in the 12 mm stage.

[1] As the lines in *Necturus* and the other Amphibians are broken up in rows of neuromasts the terms "connected with", "join", "connection" only indicate that the neuromast rows form a loose contact with certain other lines. A real connection between the lines as in such forms where canals are developed does not take place. In *Hynobius* which otherwise behaves as *Necturus* the j_1 and j_2 lines do not by far reach the infraorbital line. Their common tip lies on the middle of the cheek.

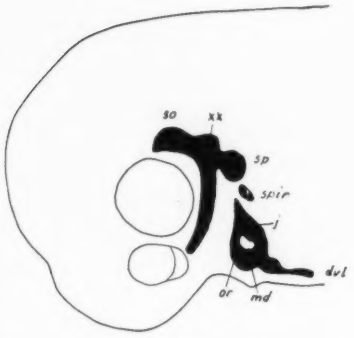

Fig. 19. *Necturus*. Embryo 12 mm. Original reconstruction.

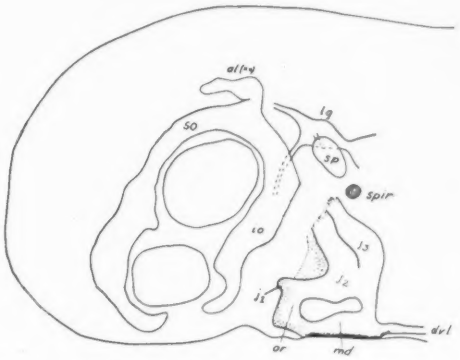

Fig. 20. *Necturus*. Embryo 15 mm. Original reconstruction.

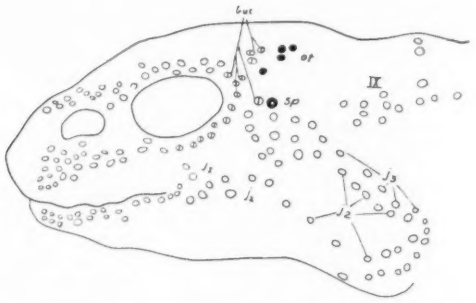

Fig. 21. *Necturus*. Embryo 24 mm. Original reconstruction made by A. JOHNELS.

In a 24 mm larva, where the neuromasts have differentiated, but, where the outlines of the neuromast groups still nearly have the shape of the outlines of their placodes, the innervation was possible to determine to a certain extent. The following statements could be made. At the posterior extremity of the supraorbital line there is a group of neuromasts innervated by the buccalis nerve (fig. 21, ⌀). They, thus, belong to the infraorbital line. Behind this group were found some neuromasts (fig. 21, •) innervated from the frontal end of the lateralis ganglion, at the root of the ophthalmic nerve.[1] This group answers to neuromasts in *Amblystoma* (according to COGHILL) innervated by the ramus oticus. The "otic" placode (*sp*) is disappearing. In one specimen it is present on one side, absent on the other, in another we could not find it at all. Its nerve, however, is retained, but does not innervate any organ, but ends in the skin.

There are, thus, two *oticus*-innervated, lateral line portions present in *Nec-*

[1] This statement depends upon a reconstruction made by dr. A. JOHNELS at the Zootomical Institute. HOLMGREN has stated the correctness of this reconstruction.

turus, one dorsal, persisting, and one ventral, disappearing. Between these portions and the glossopharyngeus-vagus lines (where the temporal line should run) there is an empty space, without neuromasts.

In *Rana pipiens* (KNOUFF 1935) and in *Pelobates fuscus* (fig. 33) the ventral of these two otic placodes is present in the young embryo and there may connect with the IX placode. As there is, however, in the *Rana* tadpole no otic nerve (STRONG 1895), it may be assumed that the "otic" placode also there disappears (or that the otic nerve has got a character which makes it undistinguishable from other nerves). In the young *Xenopus* (fig. 34) larva (6.25 mm) the "otic" placode is only suggested, and the older larva and the adult have no otic neuromasts. It therefore may be concluded that the "otic" placode is disappearing also in anurans. In tadpoles the temporal region contains no oticus-innervated neuromasts.

As already described there is at the youngest developmental stages of *Neoceratodus* (8.6 mm) a continuous cephalic portion of the main lateral line present. At the front end a portion is innervated by the facial (otic) nerve. Except this portion there is, however, another oticus innervated present, viz. the spiracular line. This line, may answer to the disappearing spiracular placode in *Necturus*. As mentioned in preceding pages the spiracular line in *Neoceratodus* extends beyond the place of the spiracle, and forms there a group of placodes which tend to join the cephalic part of the main lateral line (11.5—12 mm stages) and which continues with neuromasts at the basis of the branchial arches. These placodes, however disappear.[1]

Issuing from the preceding statements, the conditions in some *Stegocephalians*, where there are two (or three or even four) longitudinal lines which may join the temporal line, the dorsal line (when two are present) should be the real temporal line, whereas the ventral may have arisen from the spiracular line (of *Neoceratodus*) also joining the temporal line (as perhaps in *Rana*). When three such lines are present, the foremost may be an "anterior pitline" developed in a caudal direction.[2] With this explanation it is unnecessary to assume that the Stegocephalian intertemporal should be another bone than the intertemporal in other vertebrates (STENSIÖ 1937). STENSIÖ came to that conclusion, assuming that the dorsal of the two otic lines represented a "central line" (pineal line, HOLMGREN). It seems to be very farfetched to suggest that the "central line", which disappeared with the arthrodires, should reappear in the *Stegocephalians*. This "central line" must have another explanation and

[1] In *Hynobius* the "otic" placode undoubtedly develops to a persisting line of neuromasts running immediately dorsally to the locus of the spiracle. This line displays a certain tendency to join the glossopharyngeal part of the cephalic portion of the main lateral line; but no fusion occurs.

[2] In the case where there are four such lines, as in *Trematosaurus Brauni* (BYSTROW 1935), we are at a loss to explain the supernumerary.

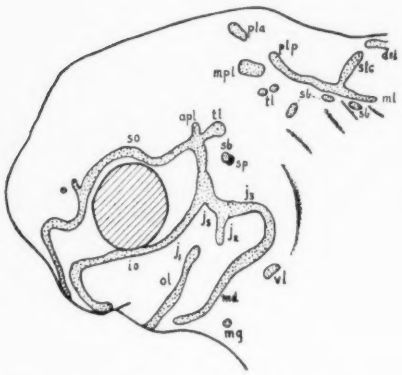

Fig. 22. *Protopterus annectens.* Embryo 13.6 mm. According to PEHRSON.

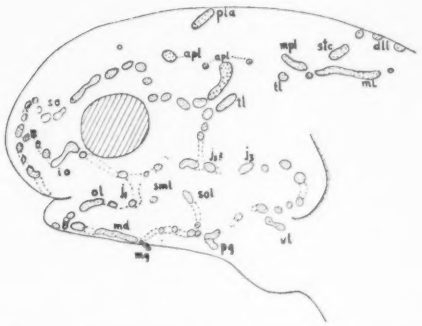

Fig. 23. *Protopterus annectens.* Embryo 17.5 mm. According to PEHRSON.

we have tried to suggest one, based upon the conditions in recent *Amphibians* and *Dipnoi,* compared with *Holoptychius.*

Our statement that the "central line" (STENSIÖ) or pineal line (HOLMGREN) disappeared with the Arthrodires, needs some explanation as STENSIÖ lately has ascribed a "central line" to palaeozoic Dipnoi. In 1936 (HOLMGREN and STENSIÖ) STENSIÖ described and figured an anterior pitline in *Dipterus platycephalus* issuing from a posterior prolongation of the supraorbital canal. This pitline is developed on the medial side of the canal (thus anterior to it) and extends to the centre of the central parietal bone. In 1947 this pitline is named the "central line" and the prolonged portion of the supraorbital canal is considered to be the anterior pitline. In *Scaumenacia* (STENSIÖ 1947, p. 138) the corresponding line issues from the supraorbital canal in front of a short "anterior pitline", but in *Dipterus Valenciennesi* (fig. 18) the "central line" is figured behind the anterior pitline. There thus seems to exist some confusion as to the "central line". If it is developed in front of the anterior pitline, it could scarcely be a "central line", which is always developed behind the anterior pitline (in *Arthrodira*). For reaching at an explanation of this "central pitline" we must resort to the ontogenetical development of the dorsal pitlines in recent Dipnoans. Fortunately *Protopterus* exhibits conditions similar to those in the palaeozoic Dipnoans. PEHRSON has made a thourough study of them in *Protopterus.* In 1942 HOLMGREN figured the dorsal pitlines of this fish. According to this picture (fig. 17) there are three line sections present, viz. an anterior dorsal lettered in the present paper (*pla*), an anterior lateral (*al*) which runs frontad parallel with the posterior part of the supraorbital line, and a short dorso-frontally directed line, the middle pitline (*mpl*), a considerable distance in front of the supra-temporal commissure. The first of these line sections apparently answers to the "central line" of STENSIÖ and the second to the

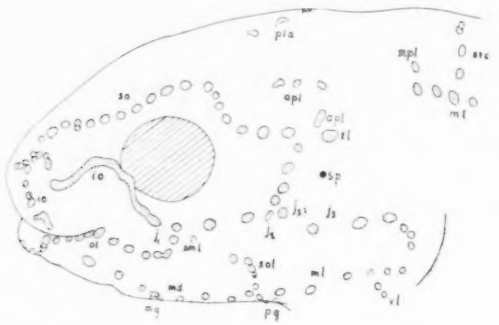

Fig. 24. *Protopterus annectens*. Larva 19 mm. According to PEHRSON.

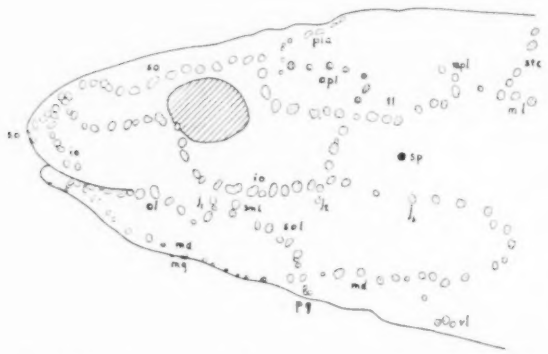

Fig. 25. *Protopterus annectens*. Larva 55 mm. According to PEHRSON.

anterior pitline. PEHRSON's ontogenetical investigation has given the following partly surprising results.

1. In a 10.1 to a 13.6 mm embryo (fig. 22) the anterior pitline arises as an outgrowth from the posterior end of the supraorbital placode. This outgrowth sucessively develops frontad into the horizontally extended second pitline section, mentioned in the preceeding lines. This line is in *Neoceratodus* always detached from the supraorbital line, but, in *Protopterus* it becomes detached late (at the 17.5 mm stage), and grows frontad as does the corresponding line in *Necturus*.

2. Simultaneously with the anterior pitline primordium, at the 12.4 mm stage, the first rudiment of the middle pit-line appears, as a big rounded placode (fig. 22, *mpl*).

3. The posterior pit-line appears as a rather strong frontally directed process from the vagus portion of the temporal line. At the frontal end of this process a placode is budded off. At the 13.6 mm stage (fig. 22) the posterior pitline thus consists of a posterior (*plp*) and an anterior (*pla*) portion. The posterior soon disappears, whereas the anterior shifts frontad, away from the rudiment

of the supratemporal commissure. In a 14 mm stage it is located dorsally to the primordium of the anterior pitline. In the 17.5 mm stage (fig. 23), where the anterior pitline consists of four neuromasts, the dorsal primordium is developing neuromasts, of which three form a pitline in the 19 mm stage (fig. 24, *pla*). In the 55 mm stage (fig. 25) this line frontally bends latero-ventrad in front of the anterior pitline. The line of which we now have followed the development, apparently corresponds to the "central line" in palaeozoic Dipnoans. It has been stated that it is innervated by the vagus nerve in *Protopterus*.

From this description it is obvious that the "central line" of the Dipnoans cannot correspond to the "central line" in the Arthrodires, but must be a special line in the Dipnoans. Its embryonic development from the posterior pit-line and its innervation make it clear that it is a detached part of this line.

SENSORY CHEEK LINES IN ANURA.

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Turning our attention to the Anurans, we have at first to correct some errors committed by earlier writers regarding the sensory lines of the larvae of non aglossan species.

In *Pelobates* the original picture of LATASTE (1874) has been reproduced and relied upon by ESCHER (1925) and STENSIÖ (1947). This figure contains at least two fundamental errors.

1. The so called angular line of ESCHER, or first portion (h_1) of the supramaxillary series of STENSIÖ, does not join the infraorbital line dorsally to the mouth, but ends abruptly at the angle of the mouth.

2. The postorbital line of ESCHER, or preopercular line of STENSIÖ, is not connected with the joined jugal and gular lines of ESCHER, or the joined second section of the supramaxillary series and the mandibular line of STENSIÖ. The two latter lines issue from a short line more or less distinctly "joined" with the infraorbital line below the eye.

Pelobates is not the most favourable object for the elucidating of the principal conditions in Anurans. In the larva of *Megalophrys* (*montana?*) (fig. 26) we have found the ideal object, where the sensory lines are developed in a quite diagrammatical way. From the infraorbital line, below the posterior part of the eye, issues an about vertically directed line (*jj*) which meets its vis-à-vis in the ventral mid-line of the head. From this line issue, on each side, two horizontal lines at some distance from one another. These lines meet below the corner of the mouth. The explanation of this arrangement is very simple. The vertical line belongs to the jugal line system, and the horizontal lines are jugo-oral and mandibular lines respectively. The ventral transversal line forms a gular portion of the mandibular line. The other investigated non-aglossan Anurans behave principally as *Megalophrys*, but there are some minor, not

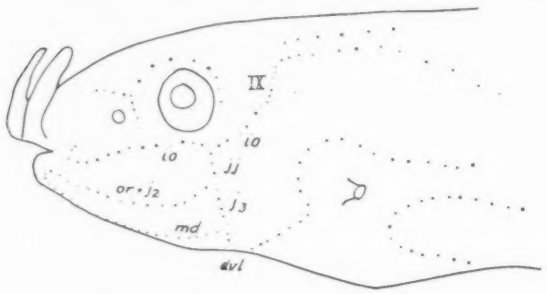

Fig. 26. *Megalophrys sp.* Sensory lines on the larval head. Original.

principal, differences. In *Pelobates* the (longitudinal) mandibular line is only preserved in its gular portion, and a transverse line joins the two oral lines, forming an anterior gular line. *Rana temporaria* behaves practically similarly, but a posterior section of the mandibular line may be present in some specimens. (In a species of *Rana* from Birma, where the adhesive apparatus remains strongly developed during the whole larval life, this apparatus has annihilated the entire mandibular line as well as both gular lines). The "connection" between the jugal line and the infraorbital is somewhat varying, not only in different species, but, also in different specimens of the same species, as for instance in *Rana temporaria*. In this frog a "postorbital line" (ESCHER) or "preopercular" (STENSIÖ) is present, but varies, as may be seen in the figures 27—31. In fig. 27 the line is developed as well defined "postorbital line", but, the jugal line is directed towards a point in front of the anterior end of this line. In fig. 31 the "postorbital line" is also well developed, caudally joining the group of "glossopharyngeal" organs. In this case the jugal line points towards the anterior end of the "postorbital line", ending, however, long before attaining it. In fig. 29 the conditions are essentially as in fig 31, but, the jugal line points anteriorly to the anterior end of the "postorbital line". In fig. 30 the "postorbital line" is well developed. The posterior end of the infraorbital line extends caudally dorsal to the "postorbital" to join the group of glossopharyngeal organs. The jugal line points anteriorly to the front end of the "postorbital line". In fig. 28 the "postorbital line" is poorly developed, consisting of 3 organs below the hind part of the eye. The jugal line points well rostrad to the frontal end of the "postorbital" line. With regard to the behavior of the "postorbital" line *Pelobates* agrees with *Rana*. What is then the postorbital line? This question is partly answered by the innervation of its organs, which takes place as far as our sections show by means of the buccalis nerve. But, also without this statement concerning the innervation the belonging of the "postorbital" line to the infraorbital series becomes quite clear with regard to the conditions in the larva of *Rhacophorus cruciger* (fig. 32). In this species the infraorbital line consists of groups of neuromasts arranged in short lines

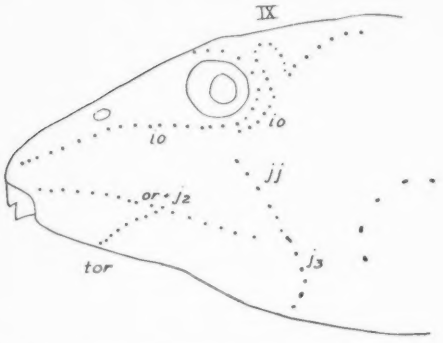

Fig. 27. *Rana temporaria.* Sensory lines on the larval head. Original.

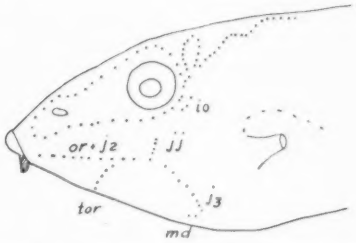

Fig. 28. *Rana temporaria.* Sensory lines on the larval head. Original.

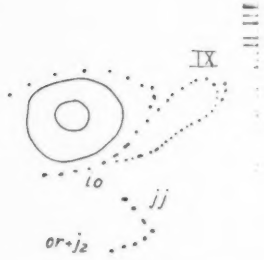

Fig. 29. *Rana temporaria.* Sensory lines around the eye in larva. Original.

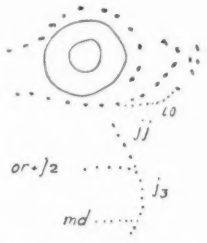

Fig. 30. *Rana temporaria.* Sensory lines around the eye in larva. Original.

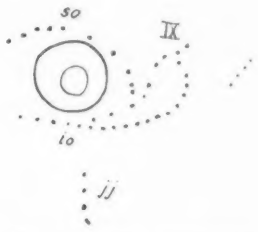

Fig. 31. *Rana temporaria.* Sensory lines around the eye in larva. Original.

perpendicular to the eye. Towards the posterior end of the eye the distal neuromasts in these rows become detached from the rest and constitute a "postorbital" line, as seen in the fig. 35.

From the preceding descriptions it is perfectly clear that there is in Anurans no preopercular line present.

The conditions in the Anuran larvae thus seem to be very simple. They built upon the early embryonic conditions, where the system of the cheek lines consist of an "inverted V" (fig. 33) as in *Urodeles* and *Dipnoans.* This embryonic structure has been retained during the prolonged larval period. As the entire lateral line system disappears at the metamorphosis, no further differentiation takes place in the non-aglossan Anurans. In the aglossan Anurans, which continue their aquatic life after the metamorphosis, a certain further differentiation seems to take place. This ends with a stage, which reminds of the Urodeles, only that certain embryonic characters are retained. The adult *Hymenochirus* seems at first sight to behave very much as *Necturus,* but there are striking differences. The double line in *Necturus,* "connecting" the post-

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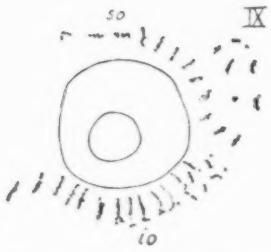

Fig. 32. *Rhacophonis cruciger*. Sensory lines around the eye in larva. Original.

Fig. 33. *Pelobates fuscus*. Embryo 6 mm. Original.

orbital part of the infraorbital line with the oral and the mandibular lines, is in *Hymenochirus* a single row of neuromast groups. There is no oral line on the mandible. It may be possible that the single row has arisen when the two limbs of a line as in *Necturus* were thrown together into one. But this seems not to be a priori certain, as the other Anurans always have a simple line in a somewhat corresponding position. Therefore it is possible that also in *Hymenochirus* embryonic conditions may be retained. The cheek system of *Hymenochirus* thus may be a part of the jugal line and a mandibular portion. The middle part of the jugal line ends frontally at the angle of the mouth, where a connection with the infraorbital line arose. This interpretation is only an uncertain suggestion as no larvae of *Hymenochirus* were available.

In *Xenopus*, where we had the opportunity of studying a great number of larvae and metamorphose stages, the sensory line system at first sight seems so strongly reduced that the anuran pattern is very obscured, but, considering its ontogenetic development we will find that *Xenopus* has retained more of the original system than any other Anuran.

In *Xenopus* as in *Hymenochirus* and *Pipa* and many other Anurans the sensory line consists of linear groups of neuromasts, generally placed perpendicularly to the extension of the lines. There are in the larva the following lines present: the supraorbital and the infraorbital lines with their usual innervation from the ophtalmicus superficialis and buccalis VII nerves respectively. These two lines meet a considerable distance behind the eye. No special otical organs have been found. In front of the common gill opening, and, extending dorsad behind the posterior part of the infraorbital line is a field with neuromast groups innervated by the IX—X nerves. The neuromasts innervated by the hyomandibular VII nerve form a group at the corner of the mouth (innervated by a special branch of the hyomandibular nerve), a line along the border of the mandible (interpreted as the oral line), at a fairly distance from it, a number of neuromast groups (the mandibular line)

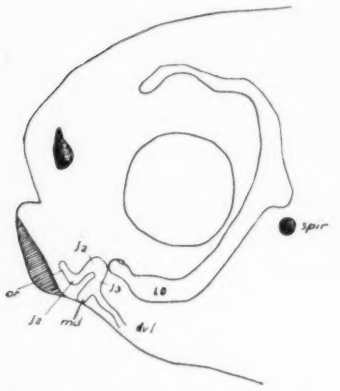

Fig. 34. *Xenopus laevis.* Embryo 6.25 mm. Original.

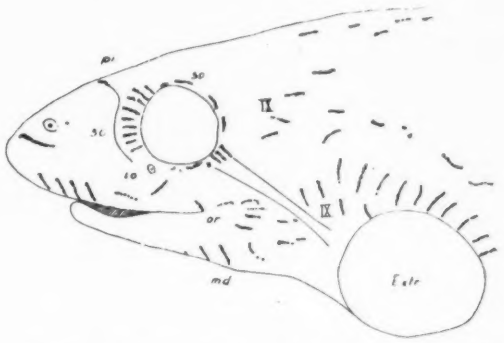

Fig. 35. *Xenopus laevis.* Just metamorphosed specimen. Original.

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extending from somewhat behind the mouth towards the ventral mid-line without reaching it, and a longitudinal line issuing from the preceding line in a backward direction. This longitudinal line reaches to a place in front of the common gill opening. All these lines are innervated by the hyomandibularis VII nerve. Comparing with the other Anurans, it is obvious that those organs which belong to the lower jaw seem to be absent in the common frog larvae. On the other side *Xenopus* seems to lack the long oral and mandibular lines and the "jugal" line. In the just metamorphosed *Xenopus* (fig. 35) the conditions are as in the larva with the exception that the long longitudinal line is totally missing.

Now, how to explain the conditions in *Xenopus?* For this purpose we must undertake an examination of the placodes in a very young *Xenopus* larva of 6.25 mm total length (fig. 34). In such a larva the sensory line placodes form continuous bands. The supra- and infraorbital lines behave as usual. There is no distinct otical part present. The cheek line system is found at the anterior end of the infraorbital placode, thus at the front of the eye. Beginning the description from in front, the cheek-line at first runs ventrocaudad, then turns abruptly dorso-caudad, and runs in that direction until it reaches the frontal end of the infraorbital line. Thence the line abruptly turns right ventrad. It then forks, sending a branch frontomediad and another caudad. The explanation of the different line portions follows immediately when comparison is made with the 15 mm embryo of *Necturus* and the 22 mm *Squalus*. The upbent part (J_2+J_3) is the jugal line, of which the anterior part (j_1) is absent (still undeveloped?). The anterior end portion is the oral line, the anterior branch at the posterior part of the jugal line is the mandibular line and the posterior branch, the subbranchial portion of the dorso-ventral lateral line (opercular line). When later the corner of the mouth shifts backward, the jugal complex

follows it caudad and the cheek lines become crowded at the corner of the mouth, without connection with the infraorbital line.

This explanation applies without difficulty upon the older larval and adult *Xenopus* and needs no further explanation.

In the same way the conditions in *Hymenochirus* and also in *Pipa* may be interpreted. In *Hymenochirus*, however, what possibly answers to the doubled up part of the jugal line in *Xenopus*, seems to develop to a single long bent row of neuromast groups, not joining the infraorbital line. This line possibly forms a secondary jugal line. By means of the conditions in this *Xenopus* embryo the cheek line system of the Anurans is bound together with that of the Urodeles and Selachians in a beautiful way.

In the cheek line system of Anurans the following points may be of importance:

1. There is no secondary preopercular line.

2. A secondary jugal line is developed. This line, possibly, consists of the dorsal portion of a jugal 2 together with a dorsal part of the jugal 3 thrown together into one line.

3. The ventral part of the jugal 2 and the oral line form a continuous line as do the ventral part of the jugal 3 and the mandibular line.

4. A jugal 1 is usually not developed.

5. The "postorbital line" of ESCHER belongs to the infraorbital line.

6. No otic part of the main lateral line exists and also no recognisable otic nerve.

SENSORY CHEEK LINES IN STEGOCEPHALIA.

It will not be necessary to discuss in detail the sensory line system on the cheek of Stegocephalians in its relations to other vertebrates as STENSIÖ has already given an explanation which essentially covers ours. STENSIÖ's views on the conditions in Stegocephalians is based on his interpretation of the cheek line system in *Holoptychius*. As will be pointed out later in this paper (p. 279) we do not dare to make use of this interpretation. Fortunately, however, *Holoptychius* is not necessary for an explanation of the Stegocephalian pattern. It is understood, and perhaps better, in comparison with Dipnoans, Urodeles and Anurans than in comparison with an incompletely known fossil which, itself, after restoration ultimately has to be explained in comparison with recent fishes.

The Stegocephalian pattern, as generalised by STENSIÖ, (fig. 36), is of lung-fish type with a differentiated jugal line, a secondary jugal, a primary oral and a primary preoperculo-mandibular line. It differs from the pattern in recent Dipnoans through the absence of the secondary cheek lines. The same explanation results from a discussion of the embryonic conditions in Urodeles and aglossan Anurans.

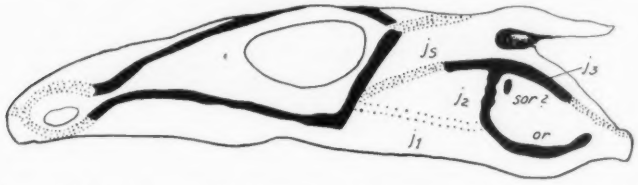

Fig. 36. *Stegocephalian.* Generalised sensory line system. According to STENSIÖ (1947).

In WATSON's reconstruction of the skull of *Palaeogyrinus* the second part of the jugal line (j_2) is represented as a line of large pits, and a similar pit is seen behind this line. It is, perhaps, too hazardous to interprete this separate pit as a homologue of the secondary oral line in Dipnoans, but, the presence of three sensory lines on the posterior end of the lower jaw in some Stegocephalians seems to indicate that a secondary oral line is not out of question in the Stegocephalians. In Osteolepids, where three such lines also occur the, originally middle of them is the secondary oral line, as will be explained later on.

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SENSORY CHEEK LINES IN POROLEPIFORMES.

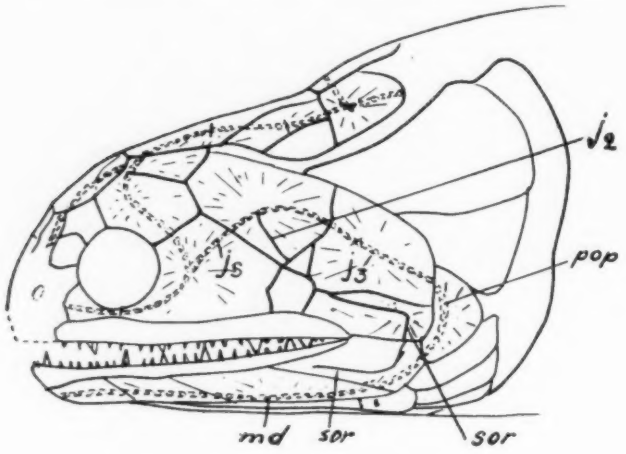
The sensory line system of the cheek in *Holoptychius flemingi* is known through the investigations of WESTOLL (1937) and JARVIK (1948). In addition STENSIÖ (1947) has published a restoration of this system chiefly based on JARVIK's specimen.

In WESTOLL's specimens (fig. 37 A) the sensory line system of the cheek consists of the long jugo-mandibular canal and two pit lines, one vertical (j_2) on the squamosal bone and one horizontal (*sor*) located on the quadrato-jugal. The former seems, dorsally, to cross the jugo-mandibular canal (according to WESTOLL's picture). The latter curves downward to the lower jaw where it is continued by a short oral pit line (*sor*).

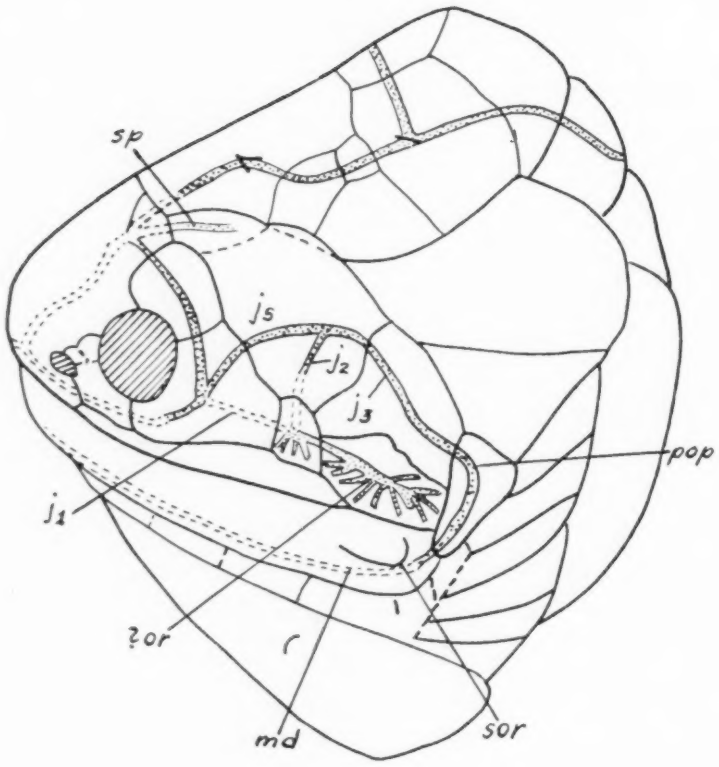
This type of system is the same as in *Dipterus,* the only difference being that in the latter fish the quadrato-jugal line "joins"[1] the lower end of the jugal canal. As has been demonstrated in the preceding pages the pit lines in *Dipterus* form the second part (j_2) of the jugal line and the secondary oral lines respectively. In consequence the pit lines in *Holoptychius* are the j_2 line and the secondary oral line. A comparison with *Dipterus* and *Ceratodus* makes clear that the proximal part of the "jugal" canal is the secondary jugal canal (*js*). As will be demonstrated below, the cheek line system in WESTOLL's description agrees perfectly with that in Osteolepiform Crossopterygians.

JARVIK's specimen (fig. 37 B) is so different from that described by WESTOLL, that one can not say, that the cheek line system even belongs to

[1] There can not be a real connection as the quadrato-jugal pit line lies more superficially than the jugo-mandibular canal.



A



B

Figs. 37 A—B. *Holoptychius*. A: according to WESTOLL. B: according to JARVIK. Lettering altered.

the same type. According to the restoration JARVIK's specimen has only the "jugo"-mandibular canal in common with WESTOLL's. There are no pit lines present. Instead there is said to be a vertical canal on the squamosal and a horizontal on the quadrato-jugal and on a small bone in front of the quadrato-jugal. On the jugal bone (infraorbital series) there are certain traces of a horisontal canal below the jugal canal. In the restoration the three canals have been drawn out to meet in the prequadrato-jugal bone (squamosal 3), and the posterior end of the quadrato-jugal canal is considered to join a pit line on the mandible. If this restoration is correct it is obvious that the jugal line consists of the same parts as in *Neoceratodus,* viz. the first jugal (j_1), the second jugal (j_2), the third jugal (j_3) and the secondary jugal (js). The oral canal, thus, is the primary oral canal. This picture of the cheek lines is so fundamentally different from that seen in WESTOLL's specimen that we are forced to feel dubious about its correctness.

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The doubts are based on the following reasons:

1. No canal pores or tubules in the sensory line system have been described or pictured except in the quadrato-jugal bone and in the small bone (squamosal 3) in front of it. The "tubes" in the quadrato-jugal bone give the impression of being no tubes but the strong radiating worn down ridges from the "growth-centre" of these bones. Similar "tubes" are seen in many of the other skull bones, viz. in squamosals, preoperculum, supracleithral as well as in the body scales.

2. The quadrato-jugal canal has been combined with the mandibular pit line which is developed just as the secondary oral line in WESTOLL's picture.

3. The existence of the j_1 canal needs confirmation, even in JARVIK's opinion.

4. Concerning the "ventral squamosal" canal (j_2) JARVIK says: "In addition to the quadrato-jugal canal ... there are traces of another sensory canal, which leaves the jugal canal in the middle part of the squamosal 1 and runs in a ventral direction, conceivably joining the quadrato-jugal canal in squamosal 3".

These many uncertainties make that we do not dare to use JARVIK's specimens in our deductions—unfortunately we may say—for they should undoubtedly add an important material to our theories concerning the cheek line system, and, perhaps, connect *Holoptychius* closer with the Dipnoans than with the osteolepiform Crossopterygians.[1]

[1] The assumption that the pit lines in WESTOLL's specimen are represented by the canals in JARVIK's (STENSIÖ) is, as yet, quite arbitrary and so is also the assumption that the pit lines should be the doubles of the canals in JARVIK's specimen. Canals accompanied by pit lines formed from the canal neuromasts proper are with certainty known only in Teleosts, but not from lower fish types. It is not correct to conclude that where a pit line runs parallel with and near to a canal it is also produced from this canal. The "accessory" pit line of the main body canal, for instance, is no double of this canal as it develops from a special placode line (fig. 2).

THE NATURE OF THE SPIRACULAR LINE (AND THE "PRESPIRACULAR" SENSORY CANAL IN HOLOPTYCHIUS).

In the following lines we will demonstrate that the "prespiracular" sensory canal in Holoptychius by no means is an isolated canal restricted to this genus. On the contrary, it is a structure of which rudiments are present in embryonic Dipnoans, in embryonic Urodeles and Anurans and perhaps also in Stegocephalians. Its occurrence in these different groups points out, really, that it must be an ancestral structure of great morphological importance.

The clue for an understanding of the "prespiracular" sensory canal and its phylogenetical derivates gives an embryo, 18 mm long, of *Squalus* (fig. 1). A reconstruction of the lateral line placodes of this shark gives a picture, which is principally the same as that of Dipnoans, Urodeles and Anurans. There is the same caudal prolongation of the orbital system as in Urodeles and Anurans, before the detachment of the "otic" sensory organ. It is also very reminiscent of the "prespiracular" sensory canal in *Holoptychius* (fig. 37 B, *sp*). The otical part of the main lateral line, when later developed, will be found dorsal to the said prolongation in *Squalus*. In *Squalus* this primordium is the rudiment of a spiracular line from the posterior end of which the spiracular lateralis organ developes. We are therefore obliged to consider the "prespiracular" canal in *Holoptychius* as a real spiracular line.

But with this statement the question as to its morphological value is not fully answered, but its morphological existence only carried down to comparatively lowly organized Gnathostomians.

The embryonic Dipnoans now enable us to carry our comparisons a step further backward into the phylogeny of the spiracular sensory line. In *Neoceratodus* PEHRSON found that the spiracular line placode developes into a line of placodes behind the spiracle. These placodes, however, soon disappear. He interpreted these placodes, as remainders of some archaic structure, not any more developing in *Neoceratodus*.

These placodes in the larval *Neoceratodus* undoubtedly correspond to a line of four neuromasts behind the spiracular organ which develop early in *Protopterus annectens*. In this lungfish the three posterior neuromasts are located upon the basal part of each external gill i.e. at the upper end of three branchial arches. The foremost of the four neuromasts thus seems to correspond with the hyoid arch. This line of neuromasts undoubtedly is comparable with the placodes in *Neoceratodus*. They are preserved longer in *Protopterus*, where external gills are present, but in *Neoceratodus*, where no external gills develop, the placodes disappear earlier.

Trying to follow up the phylogeny of the spiracular sensory line further

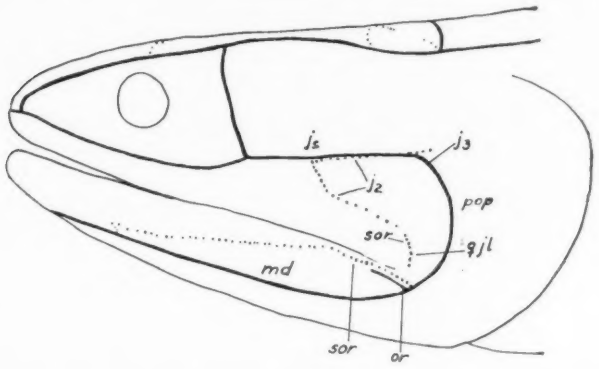

Fig. 38. *Eusthenopteron.* Sensory line system. Diagrammatical according to JARVIK (1944).

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back, we are immediately struck by its similarity with the suprabranchial line of neuromasts, situated dorsally to the branchial arches in *Petromyzon.* This line undoubtedly corresponds to the longitudinal canal which is developed along the dorsal edge of the branchio-cornual plate in *Phialaspis pococki,* recently described by WHITE (1946).

SENSORY CHEEK LINES IN OSTEOLEPIDS.

Now, turning to the Osteolepids we follow JARVIK's (1944) excellent descriptions of *Eusthenopteron* and of other Osteolepids (1948). In the terminology of STENSIÖ, the cheek line system consists of a preoperculo-mandibular line and a horizontally running pit-line (hc_2) that, from behind, follows close to the preopercular line, frontad, and then turns, abruptly, ventrad as a postmaxillary line (*orp*). The quadrato-jugal line was, probably, combined with it. On the lower jaw a dorsal pit-line runs parallel to a short canal issuing (in the infradental 4 + supraangular) from the mandibular canal.[1] The mandibular pit-line runs quite outside the short canal (SÄVE-SÖDERBERG 1933) in a specimen of *Osteolepis macrolepidotus,* and, in other specimens the short canal is, apparently, absent. The same seems to be the case in *Osteolepis panderi, Thursius* and *Gyroptychius.*

When trying to explain the cheek lines in the Osteolepids (fig. 38), we must resort to the conditions in recent lungfish, embryonic or adult, to the palaeozoic lungfishes and to the Porolepids (according to WESTOLL). These three types of fish have already been compared in preceding pages. It there was demonstrated that these types may be contained in a common pattern: the

[1] In STENSIÖ's reproduction of JARVIK's picture the pit-line erroneously is located ventrally to the short canal.

lungfish pattern. The palaeozoic *Dipterus* was compared with *Protopterus* and *Neoceratodus* and its features were derived from those of the latter. As the cheek lines of *Dipterus* (fig. 18) are about quite the same as those of an *Osteolepid*, it must be concluded that the explanation of them must be the same, viz. that the horizontal part of the "vertical pit-line" is the homologue of the second portion of the jugal line (j_2), the vertical portion and the quadrato-jugal line the postmaxillary portion of the *secondary oral line*, which in the Osteolepids continues as a pit-line on the lower jaw. The primary oral and the secondary mandibular lines are absent on the cheek. The canal which extends from the postorbital line to the preopercular plate is, as in lungfishes and *Holoptychius* the homologue of the *secondary jugal* line. The vertical portion of the preopercular line (running in the preoperculum) of STENSIÖ is the preopercular portion of the mandibular line (as compared with sharks). Here we want to mention a detail, insignificant in itself, but, which may be of comparative anatomical value. In *Neoceratodus, Dipterus* and *the Osteolepids* the jugal 2 pit-line (the "vertical pit-line") crosses over the horizontally running jugal canal about at the point where the secondary jugal merges into the jugal 3 (if the latter is not reduced). In *Polypterus* the vertical pit-line occasionally has a small portion dorsally to the horizontal pit-line. Also in *Holoptychius* such a crossing seems to be present in WESTOLL's reconstruction.

The lines on the mandible will be dealt with later (p. 287).

SENSORY CHEEK LINES IN ACIPENSER AND POLYDON.

In a 21 mm long larva of *Acipenser stellatus* PEHRSON has found a short jugal and, also, a reduced mandibular line. The jugal line lies distinctly below the spiracle and is directed frontodorsad toward the postorbital part of the infraorbital line. This pit-line, thus, either may be a secondary jugal line or part of the third section (j_3) of the primary jugal line. As it is, however, distinctly separated from the jugo-mandibular section of the latter, it is most probable that here is the question of a secondary jugal line as in *Crossopterygians*. A preopercular line portion joining the temporal part of the main lateral line behind the spiracle is not present.

Polyodon may behave as *Acipenser*, but nothing is known about the development of its sensory line system. The secondary jugal line, however, is complete and joins the postorbital line below and frontally to the spiracle.

Thus the living Chondroichthyes coincide more with the Crossopterygians than with the Actinopterygians as far as these lateral lines are concerned.

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SENSORY CHEEK LINES IN POLYPTERUS.

The early ontogenetical development of the cheek lines in *Polypterus* being unknown, we are confined to form our opinion about the lines partly from adult specimens and partly, especially, from the conditions in a 24 mm larva, described lately by PEHRSON (1947). This larva is very interesting as it demonstrates that the so called preopercular canal does not by far join the temporal division of the main lateral line but ends dorsally at the point where the "horizontal pit-line" runs off in a frontal direction. About at the same point also the "vertical pit-line" issues. In older larvae (37 mm and upwards) a dorsal continuation of the primary preopercular canal also is formed, but this continuation does not contain one single neuromast and has the character of a tube-canal, ending with a pore just below the cephalic division of the main lateral line. This dorsal part of the preopercular line is secondarily added to the primary line. In Palaeoniscids (*Glaucolepis, Boreosomus* and others) there are many pores upon the corresponding dorsal part of the preopercular canal and therefore it must have contained a fair number of sense organs.

The vertical pit-line in *Polypterus* starts as a short line dorsally at the upper end of the primary "preopercular" line. Supposing that this short line once extended ventrad joining the so called quadrato-jugal line then to continue on the lower jaw as a secondary oral pit-line, its cheek portion should correspond to the second division of the jugal line in other fishes, the third being utterly reduced or absent. Accepting these homologies, the "horizontal pit-line" must be the secondary jugal line. The first division of the primary jugal line is absent and so is the primary oral line. On the posterior half of the lower jaw there are beside the mandibular line two other lines present. These generally are considered as belonging to the oral line, bent at about right angle.

SENSORY CHEEK LINES IN ACTINOPTERYGIANS.

1. Holosteans.

The conditions we have met with in *Polypterus* and the Osteolepides lead immediately over to the Actinopterygians.

Unfortunately the earliest development of the sensory lines of the cheek is quite unknown. The very accurate pictures of the head of *Amia* (fig. 39), published by ALLIS (1889), are quite unsuitable as representing the early development, as the youngest is already 11.5 mm long and the placode stage is found in the 7 mm embryo. In the 11.5 mm young fish the sensory line system is already practically as in the adult. We have investigated the devel-

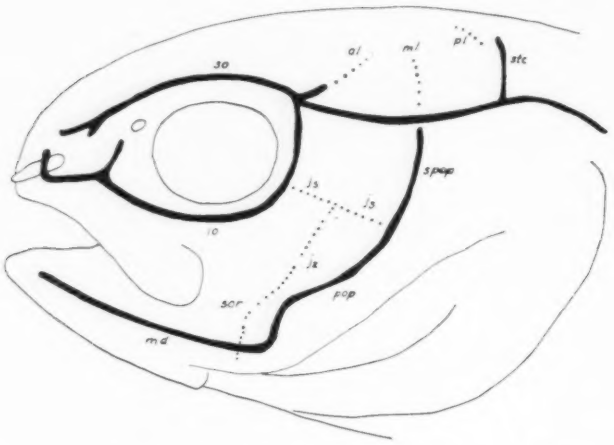

Fig. 39. *Amia calva*. Sensory line system. According to ALLIS and PEHRSON (1922).

opment of the cheek-lines in *Amia*, and make the following statements: 1. There is in the early (7 mm) embryo (fig. 40) no connection between the so called preopercular line and the temporal part of the main lateral line, this connection developing later. 2. The upper end of the "preopercular" line placode bends abruptly frontad, extending a short precess toward the postorbital part of the infraorbital line. This process, however, does still not attain the infraorbital line. Below the frontal part of this process is the indistinct primordium of the so called "vertical pit-line" (fig. 40, j_2). As to the further development (in the 8 mm stage), it is fairly evident that the vertical pit-line joins the anterior part of the "horizontal pit-line" (fig. 41) the frontal end of which later gets a connection with the infraorbital line. In the light of the preceding conclusions these conditions must be interpreted as follows: 1. the first appearing primordium is the primary preoperculo-mandibular placode, from the upper end of which issues the primordium of the third portion of the jugal line (j_3). 2. The vertical pit-line is the second section (j_2) of the same line, and its continuation on the jaw the secondary oral line (fig. 41), 3. the anterior section of the "horizontal pit-line" in front of the "vertical" represents the secondary jugal line. The first section (j_1) of the jugal line is absent. 4. If compared with *Polypterus*, where the vertical pit-line on the jaw was interpreted as the jugal 2 line together with the secondary oral line in Crossopterygians, the vertical pit-line in *Amia* ought to be a corresponding line. 5. The dorsal part of the preopercular line is a new formation not present in any non-actinopterygian fish. 6. The "preopercular line" consists, thus, of two sections: the upper section (the secondary preopercular line fig. 39) dorsally to the "horizontal pit-line" and the lower section (the primary preopercular line) which is the upper part of the mandibular line in sharks and others.

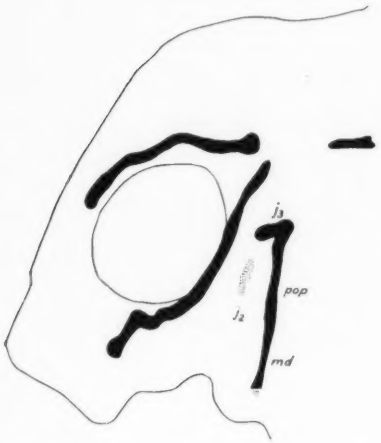

Fig. 40. *Amia calva*. Embryo 7.5 mm. Original.

Fig. 41. *Amia calva*. Embryo 8 mm. Original.

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The only knowledge of the development of the cheek lines in *Lepidosteus* we can obtain from the literature are the short notes on a 9.3 mm embryo published by HAMMARBERG (1937). According to this there is only one pit-line present on the cheek. At first it is connected with the "preopercular" line, dorsally. Later it is detached from this line, dorsally, and its ventral end joins the mandibular line at about the place where it passes to the mandibula. As the head of the larva by degrees is prolonged and the mandibular joint is carried frontad, the pit-line becomes more and more horizontal, as it is found in the adult of *Lepidosteus viridis* (WESTOLL 1937). It is obvious that this pit-line is the "vertical pit-line" or the second section (j_2) of the jugal line connected with a secondary oral line and not any "horizontal pit-line". On the jaw the oral line may be represented by the transverse mandibular pit-line. The horizontal pit-line is absent in *Lepidosteus*. The preopercular line is represented by its dorsal (secondary) as well as by its ventral (primary) portion.

2. Teleosts.

The early development of the cheek line system is not known. In Cyprinoid fishes (fig 42) (*Leuciscus, Alburnus* and others) the first line to appear on the cheek is, according to LEKANDER (1949), the lower part of the preopercular line together with the proximal part of the mandibular line. Then appear irregularly arranged neuromasts between the orbit and the preopercular line. These neuromasts probably represent the horizontal and the vertical pit-lines, but it is not possible to tell in what way they are arranged. In *Cobitis fossilis* (figs. 43 A,B), however, the conditions are more favourable

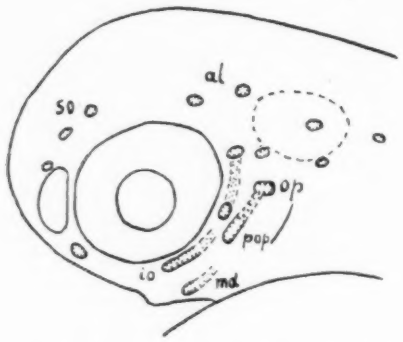


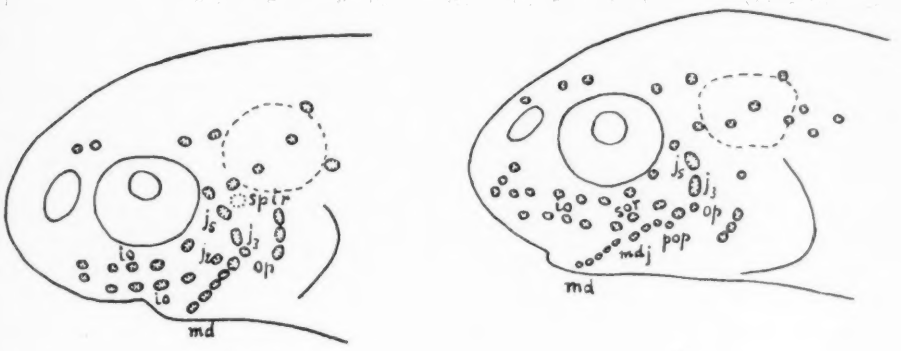
Fig. 42. *Leuciscus rutilus*. Embryo 5.9 mm. According to LEKANDER.

for an interpretation. In the youngest stage at LEKANDER's disposal, the lower part of the preopercular line, dorsally, bends gently frontad, coming in contact with the postorbital line. This curved portion of the line, obviously corresponds to the "horizontal pit-line" viz. the secondary jugal line. The vertical pit-line is represented by a few neuromasts, forming a line from the posterior end of the secondary jugal line to the region of the future mandibular joint (fig. 43 B). Later during the development this joint is carried frontad far below the eye. The vertical pit-line is prolonged at its lower end, which is, thus, carried frontad below the eye. Simultaneously the horizontal pit-line (secondary jugular line) has, by degrees, got raised up at its anterior end and consequently acquired a more or less vertical position. What sometimes is considered to be the horizontal pit-line (ALLIS), is, thus, the vertical line and vice versa.

As in *Amia*, the dorsal part of the preopercular line, when present, develops later than the ventral.

SOME REMARKS ON THE CHEEK LINES IN ACTINOPTERYGIANS.

In his paper STENSIÖ has in an admirable way collected the material of Palaeoniscids, Sub-Holosteans and Holosteans, upon which an explanation of the different parts of the sensory lines on the cheek of these fishes partly must be based. His explanations do not tally with those that we have arrived at, the differences generally depending upon the fact that we have fundamentally different views regarding the ontogenetical material upon which the explanations ultimately must rest. According to our opinion the following sensory lines may be present in the Actinopterygians: 1. The secondary jugal line (= part of the hc_1 line of STENSIÖ), 2. the second part of the jugal line (j_2) (= at least the dorsal part of the postmaxillary line, $hc_2+orp.$), 3. The third portion of the



A B

Figs. 43 A—B. *Cobitis fossilis*. A: Embryo 3.4 mm. B: Embryo 4.3 mm. According to LEKANDER.

jugal line, mostly absent or very strongly reduced (= hc_3), 4. The preopercular line, consisting of a ventral and a dorsal part, the latter postspiracular (= *poc.* in STENSIÖ's lettering) and on the lower jaw, 5. a secondary oral line portion (= the oral line orp_1) and 6. a mandibular line (= *mdc*); (hc_1 is absent and also the orp_{1d} line and the orp_{1v} in STENSIÖ's description).

In the Actinopterygians the secondary jugal line ("horizontal pit-line") mostly is not connected with the postorbital canal. It is therefore liable to shift according to the general growth of the cheek region, probably in connection with the moving frontad of the mouth (STENSIÖ) and the strong development of the cheek portion of the maxillary bone. In many Palaeoniscids and Ganoids the line shifts by lowering of the anterior end so that it becomes directed ventrally to the eye, with its anterior end located on the wide posterior part of the maxillary. As the maxillary and also the dentary in recent Chondrosteans, Holosteans and Teleosts (HOLMGREN 1942) develop in a quite different way than the other external dermal bones (sensory line bones in particular) it is very probable that the part of the secondary jugal line which is located on the maxillary cannot be responsible for the development of this bone. From this point of view we must conclude that the fronto-ventral extension of this pit-line is only the effect of growth conditions.

ON THE MANDIBULAR AND ORAL LINES IN GANOIDS AND CROSSOPTERYGIANS.

The nature of the mandibular and oral lines and their relations to one another has caused some difficulties. These difficulties depend to a great deal upon scarse, available embryological evidences. In reality the only investigations

upon which the ontogenetical development of these lines can be based, is that of Miss PLATT on *Necturus* and our own on Dipnoans and sharks.

STENSIÖ says (p. 30): "The oral line arises embryologically as a direct ventral continuation of the postmaxillary line (hc_2), growing out from it on the posterior part of the lower jaw. Here it meets and connects with the mandibular line, which is just growing forwards. More precisely, it connects with the very anterior end of the mandibular line. From their point of connection the two lines then grow out forwards together along the ventral margin of the lower jaw, a condition which probably means that in their middle and anterior portions, which runs forwards, they arise from a compound mass of epithelial cells. In their longer middle portions they normally differentiate from each other, step by step, as their outgrowth proceeds, whereas in their foremost portion they remain intimately connected, except in the majority of modern sharks. As already stressed the foremost portion of the mandibular line is therefore as a rule presumably of a compound nature." As there is nothing known about the very early development of the oral and mandibular lines except in *Necturus*, the above general statements must be a generalisation of the *Necturus* conditions. We will therefore try to investigate to which extent the conditions in *Necturus* bear up this generalisation.

As already stated, there is an incompleteness in PLATT's description, as the placodes of the oral and the mandibular line already in the earliest investigated stage of development are connected apically by thickened epithelium. This epithelium is continuous with the epithelium at the medial portion of the lower lip at a stage, where the mouth not yet has opened and becomes partly used up to cover the outgrowing mandible. When the mandible, step by step, grows frontad, the two lines also are lengthened, keeping their near relation to the lower lip. As the connecting tissue during this process remains in contact with the middle portion of the lower lip, it is certain that the length of the lines increases behind this point. It is at least no indication of an apical growth by means of cell material, belonging to the connecting portion differentiating into line portions in a frontal direction. There is no indication either in *Necturus* that the oral and mandibular lines from their point of connection "grow out forwards together along the ventral margin of the lower jaw, a condition which probably means that in their middle and anterior portions, which run forwards, they arise from a compound mass of epithelial cells".

In *Squalus*, where the oral and mandibular lines in the early embryo develop at a fair distance from one another, they seem to have no early apical connection and their growth thus is independent of any common undifferentiated tissue at their tip. They, however, both are fixed at the medium portion of the lower jaw and this connection is retained as the jaw grows out fronto-mediad. In *Squalus* (as probably in many other sharks) a certain reduction of the lines takes place already at an early ontogenetical stage. In *Chlamydoselachus*

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results a real apical connection between the two lines. In front of this connection the mandibular canal continues frontad for a short distance. There is no indication present to give evidence for this terminal canal section being of a compound nature (STENSIÖ). On the contrary the innervation of its neuromasts (ALLIS 1923) by means of the same nerve stem as the mandibular line, whereas the oral line has a nerve of its own, speaks for this apical portion of the line being throughout mandibular. Therefore it seems most reasonable to accept the view that the mandibular line simply grows out frontad, without any compound apical portion.

In *Neoceratodus* the oral and mandibular lines according to PEHRSON develop at the lower ends of the two shanks of the inverted V (8.6 mm stage), as described in preceding pages. Already in a 10 mm stage there is a tendency of the oral and mandibular line rudiments to join apically, a junction which takes place already before the 11.5 mm stage. There is also, apically, an area of thickened epithelium joining their tips. In the 10 mm stage the lower jaw is developing, and, simultaneously the lines have entered the jaw rudiment and then, step for step, lengthen as the jaw becomes larger. The definitive junction of the two lines takes place somewhat behind the tip of the oral line. In *Protopterus* the development is quite similar. In the 13.6 and 14 mm stages the oral line already surpasses the mandibular line considerably before any junction has been fully effectuated. Also in the *Dipnoi* there is no indication of the tip portion of the lines of the lower jaw being a compound structure.

The sharks, lungfishes and *Necturus* are the three kinds of living animals where primary oral and mandibular lines exist simultaneously. In the Actinopterygians the primary oral line is substituted by a secondary oral pit-line. Therefore, what may hold true concerning the interrelation of the primary oral and mandibular lines may not be applied to the interrelation between the *secondary* oral and the primary mandibular. The ontogeny has nothing to tell about the latter question as not a single Actinopterygian has been investigated regarding the development of these lines. All facts which may answer to this question must be gathered from the lines in adult specimens and from the innervation of these lines. The sensory line system of the Teleosts being very complicated as neuromasts are many times strewn out over the surface of the cheek without forming definite lines, has better be left out in this account. Then there are left only *Amia, Polypterus* and *Lepidosteus,* from which we have to gather our direct knowledge of the sensory lines of the lower jaw.

From ALLIS's (1889) drawings of young larvae of *Amia* may be gathered that the ventral extremity of the j_2 line on the cheek corresponds to the upper end of the so called transversal mandibular pit-line, which is the only existing pit-line on the lower jaw. That the j_2 line ("vertical pit-line") and the mandibular pit-line belong together is further proved by their innervation, as they have a common nerve-stem issuing from the hyomandibular nerve. For com-

parison with adult specimens it is important to remember that the mandibular canal is enclosed in the splenial bone rudiments on the ventrolateral side of the Meckelian cartilage, and, that the transverse pit-line of the jaw is formed lateral and dorsolateral to the cartilage, thus morphologically dorsal and superficial to the mandibular canal. The line of primary pores generally marks a line along which the sensory canal has invaginated.

In *Lepidosteus* the oral and the mandibular lines are largely as in *Amia*, but, with the difference that the transversal pit-line lies considerably anterior to the lower end of the "vertical pit-line" of the cheek. Also here the transversal pit-line has a special nerve issuing from the hyomandibular stem. The upper part of the vertical pit-line is innervated from the dorsal part of the hyomandibular (preopercular) nerve, the ventral part from the ventral part of the same nerve (NORRIS 1925). In the embryo the lower end of the vertical pit-line is "joined" with the preopercular line.

There are generally on the lower jaw of *Polypterus* three pit-lines, viz. a transversal, a short longitudinal and a very insignificant premandibular. The transversal and the longitudinal lines lie both distinctly dorsally to the original position of the mandibular canal and have as far as we know nothing to do with it, in spite of the transversal crossing over the latter (cf. *Amia*). The innervation of these lines tells very little about their origin as all the pit-lines are innervated through short nerve-fibres issuing from the hyomandibular nerve just opposite the line portions. Of some special interest may, perhaps, be, that the transversal and the longitudinal pit-lines of the jaw have each their proper nerve, but as these branches issue from the hyomandibular nerve closely together, we do not ascribe any great importance to it. The two lines may, perhaps, be considered as a single pit-line bent more or less at right angle, or, comparable with the pattern in *Osteolepis* where the vertical (the secondary oral) line meets the horizontal jaw line in front of the posterior end of the latter. Also the conditions in the 24 mm larva can be interpreted in this way. It is obvious that the transversal pit-line in *Polypterus* corresponds to that in *Amia*. In *Polypterus* it has, however, lost its connection with the "quadratojugal line", i.e. with the "vertical pit-line". Concerning the premandibular pit-line is only to be remarked that it receives its nerves from the nerve of the foremost mandibular line neuromast.[1] It may be possible then, that this pit-line is formed from the mandibular line and has no relation to the other pit-lines of the jaw. But it is also possible that it represents a foremost detached portion of the oral pit-line, and that is our opinion. WESTOLL (1944) has described such a premandibular pit-line in *Hoplolepis* and *Pyritocephalus* and STENSIÖ has interpreted them as a foremost portion of the (primary) oral line. STENSIÖ's opinion, probably, is correct. But we cannot share his opinion

[1] In the 37 mm specimen.

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(p. 73) "that the middle part of the oral line should differentiate throughout from the mandibular line and that thus it developed embryologically in the same manner as in fishes and Amphibians in general". As such a mode of development has never been demonstrated in any vertebrate, we cannot share this opinion. The primary oral and mandibular lines grow out independently (cf. preceding pages) or from the caudal border of a common apical primordium, of which the dorsal part produces the oral, the ventral part the mandibular line, but, most probable is that growth takes place everywhere along the lines. As exemplified by *Chlamydoselachus* and the Dipnoans the one or the other of the two line components may finish or interrupt its growth and the other continue it. Assuming that in Ganoids the secondary oral line has similar relations to the mandibular line as the primary oral line, the process may be the following. The two lines develop from two different primordia, meeting frontally. These primordia, produce an oral line portion, dorsally, and a mandibular portion ventrally. Frontally where the two primordia meet, the dorsal part of the common primordium ceases producing oral line material, whereas the ventral part continues producing mandibular line material in the same rate as the jaw grows out frontad, carrying with itself the primordium. This primordium now contains an active mandibular primordium part and occasionally a latent oral part but the line itself is throughout a mandibular line. In the cases of *Amia* and *Lepidosteus* no such oral part is present, in those of the Hoplolepids, where the oral line is represented by two markings (Stensiö 1947, p. 73), that latent part was activated again and deposited the anterior portion of the oral line. This way of explanation seems to be supported by the conditions in the Osteolepids, where the oral and the mandibular lines are separated all along the posterior 2/3 of the jaw, the oral line ending with a transversely located separate short pit-line, but the mandibular continuing further frontad. If the oral line primordium ceases to produce oral line material during the middle period of its development, the conditions in the ganoids above named would result. The result of this discussion is that the middle part of the mandibular line is no compound part, but is a pure mandibular line in *Polypterus*.

We will now take up the question of the three lines on the jaw of the Osteolepids. These lines are, counted from the dorsal side: the oral pit-line (or dorsal oral line), the oral canal (or ventral oral line) and the mandibular line.

As there is no evidence for the assumption that the two oral lines have arisen by the splitting up longitudinally of a preexisting primary oral line, we must discuss the two lines as separate structures and from this point of view try to explain them. In *Eusthenopteron*[1] and other Osteolepids the dorsal line is a

[1] Cf. the foot-note on p. 281.

long pit-line that sometimes runs uninterruptedly from the posterior end of the mandible to the foremost third of the jaw, there ending with a transverse line. The oral canal is a short canal in the posterior part of the jaw. It is continuous with the mandibular canal posteriorly. As the oral line is superficial and the mandibular canal embedded in the infradental 4 (splenial 4 + supra-angular) bone, one cannot say that it is connected with the mandibular line as it seems to be in some restorations. STENSIÖ says about the pit-line that it generally runs just outside the oral canal, "there is every reason to believe, however, that in embryos it lays ventrally to it" (p. 84).[1] We also believe that the original position of the pit-line was ventral to the oral canal. Our direct evidence is, however, not very strong and is restricted to JARVIK's figures 68 E and D of lower jaws of *Tursius pholidotus*. In fig. 68 E the oral canal and the posterior part of the mandibular canal are seen. Also the oral pit-line, broken up in segments, is represented there. In 68 D the pit-line is represented as broken up in segments, of which the most posterior seems to have been located ventrally to the oral canal, if the two figures are combined. This is the only direct evidence we have been able to detect for the assumption that the pit-line originally was situated ventrally to the oral canal.

In some Stegocephalians (BYSTROW 1935 and NILSSON 1944) two other canals are simultaneously present besides the mandibular canal, both of them joining the latter. The dorsal of these canals (Sulcus accessorius sensorialis, NILSSON 1944) is short, the ventral is a long one, extending nearly to the tip of the mandible. The dorsal canal may correspond to the oral canal in the Crossopterygians, the ventral to their oral pit-line. In *Dwinosaurus tertius* the short dorsal canal (the primary oral canal) is absent, but the two others strongly developed. In *Benthosaurus* the short dorsal canal seems to join the oral line (BYSTROW 1935, fig. 14, p. 89 and fig. 35 A, p. 131). These canals undoubtedly represent the three lines of Crossopterygians (cf. STENSIÖ 1947, p. 97).

When reviewing the sensory line conditions on the lower jaw, one is struck by the occurence of but two lines in the middle and anterior parts of the jaw, even if a supernumerary line is found leaving the cheek with a general direction to the jaw. In the living Dipnoans the secondary oral line undoubtedly is destined to the jaw, but there is no special jaw line developed for the reception of this line. There are only the two normal (oral and mandibular) lines present. In *Protopterus* the secondary oral line from the cheek joins the mandibular line, and there are, thus, also only the two primary lines present on the jaw. In the Crossopterygians and the Stegocephalians, where three lines are present on the posterior end of the jaw, there are also only two lines present in the middle and anterior part of the jaw. These evidences seem to speak for the

[1] In JARVIK's representation of the head of *Osteolepis macrolepidotus* partly reproduced from SÄVE-SÖDERBERG (1933), the pit-line is located quite outside the canal.

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assumption that these two lines are the primary oral and mandibular lines respectively. When secondary lines reach the lower jaw, these lines do not continue as separate jaw lines but join any of the two ordinary primary lines.

As mentioned in preceding lines (p. 291) there are three sensory lines present at the posterior end of the lower jaw in Osteolepids and Stegocephalians. The two of them are oral lines which both are said to join the mandibular line at the posterior end of the jaw. As already explained the originally dorsal one of these oral lines is the primary oral line and the ventral one, the secondary oral line.

Now it remains to explain how the primary oral line could reach the mandibular line without crossing the secondary oral line, which once must have formed an unbroken line from the quadrato-jugal to the jaw. As lines crossing each other at *the same level* do not occur, the actual connection between the primary oral canal and the mandibular canal must have taken place when there was no secondary oral line developed between the primary oral and the mandibular canals, i.e. either before the secondary oral line was developed or in an area where the secondary oral line was not developed at all. Such an area is present in such Osteolepids, where no connection exists between the quadrato-jugal line and the mandibular pit-line (secondary oral line). In this area the primary oral line could grow, caudad, ultimately joining the mandibular canal. The connection between the secondary oral line and the mandibular line was established simply by the caudal part of the oral pit-line growing caudad, as it has really done in Osteolepids. In the Stegocephalians, where the secondary oral line probably was developed as a canal, there could result a real connection with the mandibular canal. But this explanation presupposes that the quadrato-jugal canal in Stegocephalians does not reach the lower jaw, but, joins the mandibular canal dorsally to the mandibular joint. Such a junction, however, does not seem to be known in Stegocephalians, but the direction of the caudal part of the quadrato-jugal canal (primary oral canal) seems to indicate the possibility of such a junction for instance in *Palaeogyrinus*. In this species WATSON has figured a small detached line portion caudally to the second portion (j_2) of the jugal line. This small sensory line-marking on the cheek may, perhaps, represent the cheek rudiment of the secondary oral line as already suggested.

SENSORY CHEEK LINES IN HOLOCEPHALIANS.

The conditions of the cheek lines in *Chimaera* are very simple and offer no difficulties and need no detailed discussions. It is obvious that the explanation of this system must be based on a comparison with such embryonic sharks, where the system is not yet differentiated, and, not with adult fishes or older

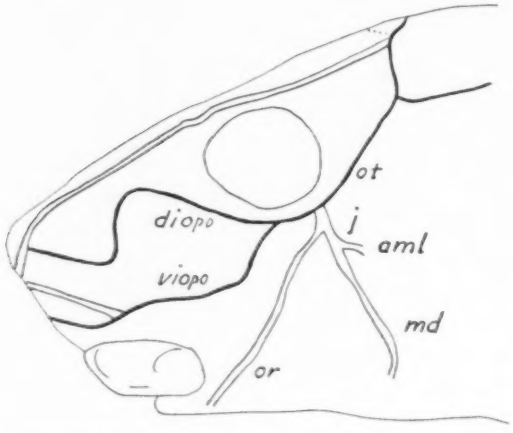

Fig. 44. *Chimaera monstrosa*. A variant of the sensory line system. Original.

embryos of sharks and urodeles. HOLMGREN (1942) tried to make a comparison on the basis of some embryonic stages of *Squalus*, but at that time his knowledge of these stages was not sufficient. At that time the 18 mm stage was missing and that stage is important. At that stage the system consists of a horizontal placode ending caudally with a small knob. From this placode issue, a little behind its frontal end, the oral line, and, caudally, the mandibular line. The horizontal placode represents the undifferentiated jugal placode. Its anterior end portion is the future first jugal subdivision (j_1) and the rest of it the undifferentiated second and third subdivisions (j_2 and j_3).

In some specimens of *Chimaera monstrosa* (fig. 44) the cheek line system issues from the anterior end of the oticus-innervated part of the main lateral line and consists of a short line which soon branches into two, both running to the lower jaw. The anterior one is a primary oral line, the posterior a primary mandibular line. A short distance from the basis of the posterior line issues sometimes the rudimentary ampullar line. If compared with the 18 mm *Squalus* embryo it is apparent that this ampullar line corresponds to the disappearing knob (postjugal twig in *Chlamydoselachus*) at the boundary between the jugal line and the mandibular line (cf. STENSIÖ, p. 39 and 40), this knob probably representing the remainder of the cephalic part of the dorsoventral lateral line, as sometimes present in *Protopterus*.

It is of a certain importance to point out that there are no traces of any "supramaxillary lines" in the space enclosed by the oral- and jugalo-mandibular lines in any Holocephalian. In reality there could not be any such traces, as the jugal line itself must represent the supramaxillary series also in Holocephalians.

From what has been told previously, it is perfectly clear that there is no preopercular line present in the Holocephalians (contrary to STENSIÖ's inter-

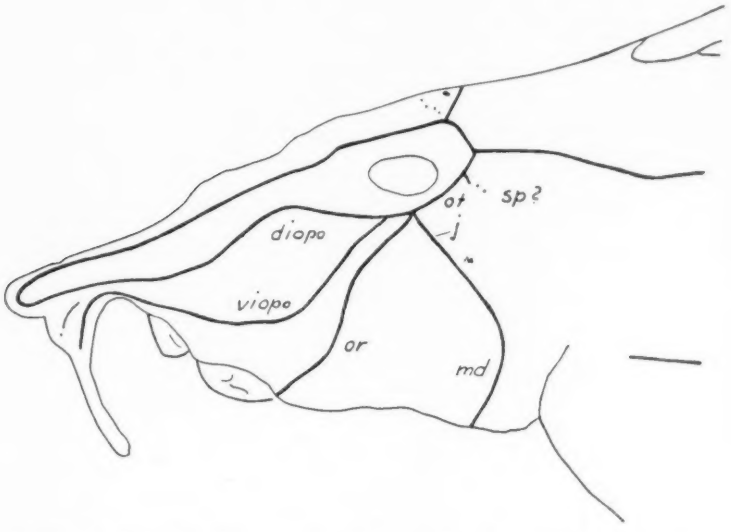

Fig. 45. *Callorhynchus antarcticus.* Sensory line system. According to HOLMGREN (1942).

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pretation, according to which the jugo-mandibular line is said to be a preoperculo-mandibular line).

In 1942 HOLMGREN described a rudimentary line in a specimen of *Callorhynchus* (fig. 45), which issued a little behind the mid of the oticus-innervated portion of the infraorbital line. As there is in the Holocephalians no glossopharyngeal[1] or vagus portion of the main lateral line in front of the supra-temporal commissure, the rudimentary line belongs clearly to the cheek region and can not be a rudimentary (vagus-innervated) scapular line, as STENSIÖ seems to believe. HOLMGREN has denoted this rudiment with a question-mark as a preopercular line. Since, however, the "preopercular" line in *Squalus* has been interpreted as a part of the jugal line, there must be looked for another explanation of this rudiment, if it is not simply an aberration without any morphological significance.

Supposing that this rudiment, really, has a morphological importance, it must be compared with the similary located "preopercular" line in the Arthrodires (fig. 46), as HOLMGREN supposed in 1942. In the Arthrodires the "preopercular" line issues from the hindmost part of the probably oticus-innervated part of the main lateral line (infraorbital line), in the *Holocephali* anterior to the hindmost portion. Logically must be admitted that if the Holocephalian line is a scapular line, so is the Arthrodiran also to be considered as a scapular line and if the "preopercular" line in the Arthrodires is really a preopercular line

[1] COLE's description of a glossopharyngeal organ in front of the supra-temporal commissure does not tally with HOLMGREN's results.

so must that of the Holocephali also be a preopercular line. But in the *Holocephali* the preopercular line, according to STENSIÖ, is present as a line issuing from the foremost part of the oticus-innervated portion of the infraorbital line and according to our opinion a part of the jugo-mandibular line. There is thus a fundamental difference in opinions, which will be considered when the Arthrodira and the Antiarchi are dealt with (p. 298).

SENSORY CHEEK LINES IN RAJIFORMES.

The analysis of the cheek line system in rays carried out by STENSIÖ has led him to hold opinions concerning these lines which are in the main, very different from those put forward by HOLMGREN (1942). STENSIÖ's interpretation is dominated by his interpretation of the cheek lines in sharks, according to which these are formed by the "supramaxillary" line together with a preopercular line. In the preceding pages we have, however, shown that there were certain errors committed, in the description of the ontogenetical development in sharks. These errors have caused the misinterpretation of the cheek system in sharks and also of the conditions in rays (and Holocephalians). As was stressed earlier in this paper, there is in sharks no supramaxillary line. What has been called the supramaxillary line is the jugal line, which differentiates into three sections (j_1, j_2 and j_3), the so called "preopercular" line being the third of these sections together with the dorsal (preopercular) part of the mandibular line.

Thus we maintain the correctness of HOLMGREN's earlier interpretation of the cheek lines in *Torpedo* (fig. 46). There are two such lines: the oral line and the jugal line. The jugal line is principally the same as in sharks but with the difference that it does not send off any mandibular line. In comparison with the shark embryo, the jugal line at least practically lacks its anterior section (j_1) and consists of the not differentiated second (answering to STENSIÖ's second section of the supramaxillary line) and third sections (answering to the "preopercular" line in sharks). To these constituents is added in rays the long line, which joins the scapular line. This prolongation probably corresponds to the post-jugal rudiment in the *Squalus* embryo and in the adult *Chlamydoselachus* (cf. STENSIÖ, p. 45), which probably is the cephalic section of a subbranchial lateral line (the dorsoventral lateral line), as in *Protopterus*.

The second and third sections of the jugal line in the *Torpedo* embryo are not differentiated from each other, but, it could be suggested that the vertical part of the line may be the homologue of the second section or the so called "middle cheek line" in sharks, and the horizontal part, not delimited caudally, the third section answering to the so called preopercular line in sharks, but that would, perhaps, be to make a too detailed use of the reconstruction in fig. 47.

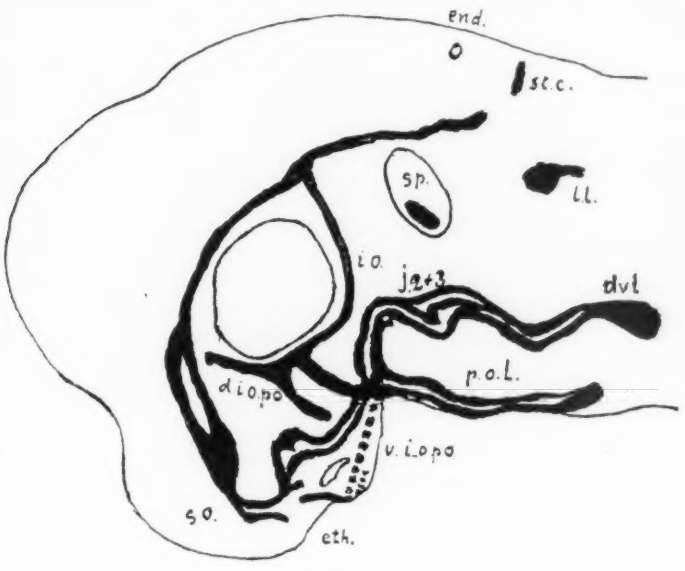

Fig. 46. *Torpedo ocellata*. Embryo 12 mm. According to HOLMGREN (1942).

It is not certain that the bend of the line in the *Torpedo* embryo really corresponds to the bend in the corresponding shark line. It is generally not advisable to make a detailed use of reconstructions of embryonic conditions, then there is always a certain variability to be considered.

HOLMGREN (1942) has pointed out that the cheek line pattern in the *Torpedo* embryo is more reminiscent of the conditions in Holocephalians than of those in sharks. In reality it has very little similarity with those in sharks, where the jugal line is strongly differentiated already in 22 mm embryos. In the rays it is not differentiated at all, and very little in Holocephalians. That the oral and jugal lines issue from the infraorbital line without a common stem is a condition which is usual in Holocephalians, but seems never to occur in sharks. That the oticus-innervated part of the infraorbital line extends from the supratemporal commissure to below the eye in rays as well as in Holocephalians, but not in sharks, also speaks for a nearer relationship between rays and Holocephalians than between the former and the sharks. The existence of the anterior (dorsal) infraorbital line in the *Torpedo* embryo and in the adult Holocephalians but not in the sharks strengthens the said relationship considerably. As there is no "preopercular" line as defined by STENSIÖ in the rays is of no consequence, as there is no such line neither in Holocephalians nor in sharks. Besides, that line in sharks is the third section of the jugal line, and thus no real preopercular line. STENSIÖ has tried to compare the big loop of the infraorbital line on the snout part in rays with a loop formed by the

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corresponding line in sharks, but admits that the loop in sharks is not the homologue of that in rays. This conclusion is undoubtedly correct, as there is no such loop in *Chlamydoselachus*, as STENSIÖ has pointed out. It may here be added that it is also absent in *Notidanid* sharks, as in *Heptanchus*, *Hexanchus* and *Notorhynchus*. The loop in rays is said by STENSIÖ to correspond with a loop of the infraorbital line in Holocephalians. But that comparison is doubtful, as the loop when really present in Holocephalians, belongs to the anterior (dorsal) branch of the infraorbital line, whereas it in rays belongs to the ventral branch (the infraorbital line proper). The anterior (dorsal) line, besides, is only present in the young ray embryo as an undifferentiated, later disappearing placode (diopo). Thus it is apparent that the loops have arisen independently in the three groups of fishes, a possibility which has also been admitted by STENSIÖ.

SENSORY CHEEK LINES IN ARTHRODIRA.

The interpretation of the cheek-lines in *Arthrodira* offers difficulties surpassing those of all other fish groups. This depends largely upon the fact that the few cheek lines in Arthrodirans have but a short extension and, thus, can not tell anything definite about there ultimate destination. Thus the field is open for hypotheses and possibilities as in no other class of fishes.

Following the infraorbital line (fig. 47) from below the eye and caudad we meet below the eye and on the suborbital plate the groove of the oral line. In *Homostius* (HEINTZ 1933) this line bifurcates on the said plate, but in all other Arthrodira it is simple. Posterior to the suborbital part of the infraorbital line follows the postorbital. This part meets (the otical part of) the main lateral line at a right angle on a level with the upper part of the eye, and seems here to be continued in a dorso-medial or caudal direction by the pineal line (HOLMGREN 1942, later called by STENSIÖ 1942, the "central sensory canal groove").[1] The anterior (otical) portion of the main lateral line is a long straight longitudinal line section which suddenly bends dorso-caudad to reach dorsally to the region of the occipital condylus. At the bending point of the cephalic part of the main lateral line a line section issues, directed ventrad or ventro-caudad. This section ends either already on the cheek or near

[1] The ground why STENSIÖ does not accept its homology with the pineal line in *Petromyzon* and the rudimentary and disappearing trigeminus placode in *Squalus*, *Amia* and *Lepidosteus*, is its position far from the pineal plate in Arthrodires. As this line has no other morphological connection with the pineal organ than that its medial end lies behind this organ, the difference in distance between this end and the pineal organ is of no consequence. Of great importance is that it begins where the placode is located in *Squalus* etc. and ends behind the pineal organ. As long as it has not been stated that the line in Arthrodirans is not innervated from the trigeminal ganglion, it must be termed the pineal line.

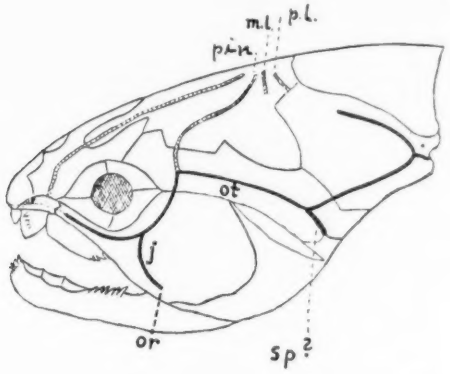

Fig. 47. *Coccosteus decipiens.* Sensory lines on the head. According to HEINTZ (1931).

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the ventro-caudal border of the cheek. In some Arthrodires (as for instance in *Pholidosteus* and *Brachiosteus*) this line is absent. It is generally called the preopercular line. That portion of the cephalic part of the main lateral line lying posterior to the "preopercular line" probably was innervated by the glossopharyngeal or vagus nerves, but, that is not stated. In front of the endolymphatic duct the lateral line receives the posterior pit-line of the skull roof and posterior to the duct the supra-temporal commissure, when present.

The greatest difficulties for explaining the cheek-lines offers the "preopercular line". The only characteristics of this line is that it is clearly post-spiracular or at least supraspiracular, that it always ends on the cheek, many times attenuated and by degrees disappearing caudally or ventrally on the cheek. There is no sign either of its bending markedly caudad nor frontad after leaving the cheek, if it really does so.

Now the question arises: Is this "preopercular line" a preopercular line in the same sense as the preopercular line in Actinopterygians?

It is obvious that it must be compared with the dorsal late outgrowing part of the preopercular line. Apparently there can be no objection raised against this homology—from topographical point of view. From phylogenetical point of view a very grave objection is to be made. In all lower gnathostomian fishes: Selachians, *Rajiformes, Dipnoi, Chondrostei* and Crossopterygians no such preopercular line is known. Therefore it is very unlikely that the Arthrodirans, amongst which the ancestors of all these groups are supposed to be found should have such a preopercular line which otherwise appears at first in *Polypterus* and Palaeoniscids, viz. in Actinopterygians. This consideration leads to the conclusion that the "preopercular line" in Arthrodirans is another line than the dorsal portion of the preopercular line in higher Teleostomians and that the two lines have developed independently in the two cases. If so is the case, and that is not to be doubted, there is no real reason to believe that the

arthrodiran preopercular line continued frontad as a long mandibular line, never stated to have been present in connection with the lower jaw of these animals. A comparison with a Holocephalian: *Callorhynchus*, can possibly give some elucidation of the arthrodiran "preopercular line" as already mentioned. STENSIÖ has interpreted the *Callorhynchus* line as possibly a scapular line. That it can not be such a line needs no other argumentation than that it issues from near the middle of the otical part of the cephalic division of the main lateral line and therefore must have been innervated by the VII nerve. In order to etablish the possible homology between the Holocephalian and Arthrodiran line in question, it is very useful to compare the course of the other lines of the posterior part of the head, beginning with the otic part of the main lateral line. In *Callorhynchus* this part begins below the posterior part of the eye, where the oral and jugo-mandibular lines issue about at the same point. From there the line turns dorso-caudad. A little behind its middle it forms a not very pronounced angle and from this angle issues the rudimentary line previously considered. From this angle the line runs further caudad in a little more dorsal direction than its ventral section. The innervation of the posterior section is not known in *Callorhynchus*, but in *Chimaera* it is otical. Then comes the point from which the lateral body-line issues. From this point also issues the supratemporal commissure, which is a very long commissure, forming a marked angle with the cephalic lateral line. In the Arthrodirans the oticus-line probably begins on a level with the upper part of the orbit. It is a long line which forms a very pronounced angle with the postotic part of the lateral line. At the angle issues the "preopercular" line. The postotic line section is about as long as the otic. It is possibly innervated by the glossopharyngeal (in *Kujdanowiaspis*, STENSIÖ 1945) and vagus nerves.[1] Then follows the point where this line meets the posterior pit-line of the top of the head, the supratemporal commissure and the lateralis line of the trunk.

If we accept this method of comparison it is obvious that the rudimentary *Callorhynchus*-line and the "preopercular" line in the Arthrodires are homologous. Anyhow, the nature of this line can only be defined negatively.

1. It is no preopercular line.

2. It is no line with continuation on the trunk or on the mandible.

There is, thus, only one line left with which it may be compared, viz. the spiracular line. As we have seen the spiracular line may issue from the otic part of the main lateral line as in *Dipnoi*. It may be present, also, behind the spiracle (*Neoceratodus, Protopterus*). Its proximal part, always, runs dorsally to the spiracle.

The location of the spiracle is very uncertain in the Holocephalians, but, it ought to have been situated somewhere in the area between the rudimentary line

[1] These innervations are by no means certain as they are pure reconstructions. It may be possible that the innervation is entirely vagal.

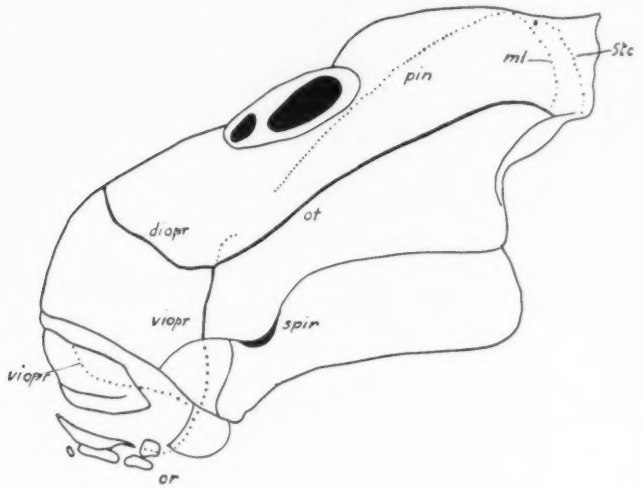

Fig. 48. *Bothriolepis canadensis*. Head, according to STENSIÖ (1947).

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and the jugal system. In the Arthrodires the spiracle has been located at about the dorso-caudal border of the suborbital plate, thus, in a corresponding place.

Evidence, hence, speaks strongly in favour of our opinion that the so called preopercular line in the Arthrodires is the spiracular line.

SENSORY CHEEK LINES IN ANTIARCHI.

In 1942, (1 and 2) HOLMGREN attempted to give evidense for the Antiarchi as being more primitive than the Arthrodirans and tried to make a comparison with Arthrodirans and with certain agnathous fishes: Cyclostomes, Cephalaspids, Pteraspids and Myxinoids. This comparison concerned the dermal skeleton, the position of eyes, nostrils, pineal organ and the sensory line system, and was extended also to the lower jaw system in Myxinoids and *Antiarchi* (1942, 2).

As to the dermal bones HOLMGREN pointed out that a strict homology could be maintained between Arthrodirans and *Antiarchi* only in a few points. The new investigations of STENSIÖ do not contradict this statement, even if some modifications may be suggested. But we will not here enter upon this question. The position of eyes, nasal opening and pineal organ are that of a Cephalaspid or of *Petromyzon* and not at all as that of an Arthrodiran.[1] There are no real indications for a shifting of the constituents of this complex from arthrodiran locations to antiarchian. Such a "shifting" is quite hypothetical, as is

[1] The Rhenanids may possibly be an exception, but they are still too imperfectly known for here to be considered.

also a shifting in the opposite direction. Our comparison of the jaws of Myxinoids and those of *Antiarchi* and Holocephalians (HOLMGREN 1942, p. 230), of course, is incomplete as the ontogenetical development of the jaw structures in Holocephalians is unknown. The question of the nature of the bones of the antiarchian jaw apparatus, if dermal bones or perichondrial, does not seem to be settled with certainty,[1] but is of no consequence as to the value of our theoretical conclusions. HOLMGREN's discussion of these questions in 1942, 2 tended (p. 236) "to the opinion that the Arthrodires are developed from more antiarchian-like than arthrodiran-like ancestors and that there is a considerable gap between the two groups, (cf. GROSS 1941). The Arthrodires are unquestionable Gnathostomians, whereas it might be discussed whether the Antiarchi really are Gnathostomians. It must be questioned at least, whether there are not sufficient reasons for considering them to be pre-Gnathostomians. Thus I am inclined to reverse the phylogenetical development, proposed by STENSIÖ, and assume that the characters of the arthrodiran head armour, position of eyes, nostrils etc. is the result of a far-reaching transformation of the conditions in hitherto unknown archaic Antiarchi . . ."

The conditions of the sensory line system undoubtedly favour this view. As is well known the infraorbital line in *Antiarchi* (fig. 48) divides in the lateral plate on a level frontal to the eye into two branches: one ("suborbital anterior branch", STENSIÖ), which forms a commissure in the premedian plate (*diopr*), and another ("suborbital part of the infraorbital line"), which runs ventrad, then bends sharply mediad and passing through the mental plate probably forms a commissure (*viopr*) below the frontal edge of the premedian plate. From the lower end of the vertical part of the ventral branch of the infraorbital line issues a line for the lower jaw. Of the two branches of the infraorbital line STENSIÖ says: "The postorbital part of the infraorbital line . . . gives off a long suborbital anterior branch, which corresponds exactly to the suborbital anterior branch of the infraorbital line in Holocephalians and embryonic rays and the anterior suborbital loop of the infraorbital line in sharks. Ventrally to the said anterior branch the remaining principal portion of the postorbital part of the infraorbital line in the *Antiarchi* runs vertically downwards, passing over into the suborbital part of the line in the same manner as in Holocephalians and rays. As may thus be gathered, the agreements with regard to the infraorbital line between the *Antiarchi*, Holocephalians and rays is very striking and far-reaching. It is nevertheless fully evident that we are concerned here with a parallelism."

These comparative morphological statements of STENSIÖ have a very limited value because it is "fully evident that we are concerned here with a parallelism".

1. The "suborbital anterior branch" of the infraorbital line is no exact

[1] The bones of the second row may be dermal and those of the third perichondrial; in both cases they may rest upon cartilage or be ossified cartilage.

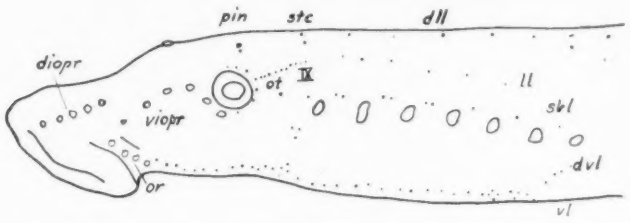

Fig. 49. *Petromyzon fluviatilis.* According to HOLMGREN (1942).

homologue of the "suborbital anterior branch" in rays, as it lies between the nasal opening and the mouth in the *Antiarchi*, and is, thus, *prenasal*, whereas it lies between the eye and the nasal opening in the rays, thus postnasal. In adult rays there are two prenasal commissures present. This fact, perhaps, may invite to a comparison with the *Antiarchi*, and in 1942, 1 HOLMGREN accepted this invitation not considering that there is in the embryo but one, the ventral, of the two commissures present, the other, the dorsal one, developing later as a secondary commissure.

2. The "suborbital anterior branch" as well as the suborbital part of the infraorbital line in the *Antiarchi* both lie between the nose and the mouth, and are, thus, prenasal, whereas the similarly named lines in the Holocephalians both lie between the nose and the eye, thus are *postnasal* (cf. HOLMGREN 1942, b).

This disagreement between the lines in Antiarchi, rays and Holocephalians is too great as to allow homologisation, and, thus, cannot give any reliable explanation of the conditions in the *Antiarchi*. This was perfectly clear in 1942, and it made HOLMGREN look for other ways for an explanation. In *Petromyzon* he then found a sensory line system, which satisfies the claims of necessary agreement. In *Petromyzon* (fig. 48) there are two infraorbital lines, innervated by two quite different branches of the buccalis VII nerve. Both these lines are prenasal. In the *Ammocoetes*-larva of *Petromyzon* the dorsal of these lines bends strongly mesiad at its frontal end, so strongly in fact, that a commissure is nearly established. In addition to these two infraorbital lines there is a "hyomandibular line" forming a more or less right angle with the posterior (lower) buccalis line. The hyomandibular line is innervated by the hyomandibularis VII nerve and, therefore, must belong to the mandibular system, probably as an oral line.

The relations of the sensory line system in *Petromyzon* with that in Cephalaspids and other *Agnathi* was dealt with in HOLMGREN's paper of 1942, 1, and will not be repeated here.

There, thus, are agreements, which may be fundamental, between the *Antiarchi* and agnathous fishes as to the anterior part of the sensory line system. As to the rest of the system, there is much disagreement. The long postorbital

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part of the otic line in *Antiarchi*[1] has no counterpart in *Petromyzon*, where this part forms the anterior portion of a normally placed portion of the cephalic part of the main lateral line. The pit-lines on the dorsal surface of the head in the *Antiarchi*, except the pineal line, have no counterparts in *Petromyzon*. On the other side there are such pit-lines present in Cephalaspids and especially in *Heterostraci*, which may answer to those in gnathostomian fishes, and it is not excluded that the *Antiarchi* as well as the *Arthodira* and all other fishes may have inherited their dorsal pit-lines from agnathous ancestors. In 1942, a, HOLMGREN has tried to point out the possibilities of a comparison between the sensory lines in *Agnathi* and *Gnathostomata*. This attempt was not successful in the details and must be revised in the light of new discoveries of paleontological and ontogenetical importance. Such a revision will follow at the end of this paper.

HOLMGREN's opinion regarding the cheek lines in the *Antiarchi* has not changed from 1942, 2 and is consequently the following: There are two prenasal branches of the infraorbital line, answering to the two buccalis line portions present in *Petromyzon*. There is but one line found on the mandibula, viz. the oral line, probably answering to the "hyomandibular" line in *Petromyzon*. If there was also a mandibular line present, this line must have arisen as a branch of the oral line, probably issuing between the infraorbital plate and the posterior plate of the second row of mandibular plates, these plates being considered by STENSIÖ as sensory line bones. There were no preopercular and no supramaxillary lines present, but the presence of the oral line includes the possibility of a jugal (j_1) line probably being included in the basal part of the oral line.

THE PREOPERCULAR LINE.

The preopercular line—when complete—is a line of neuromasts generally extending from the mandibular joint, ventrally, to the cephalic part of the main lateral line, dorsally. In adult fish this line has strong relations to the preopercular bone and has its name from that bone.

The development of the preopercular line has been studied in detail by PEHRSON in *Amia* (1922 and 1940). From his description the following statements are gathered.

1. The preopercular bone of the adult fish contains seven neuromasts.
2. In a 13.8 mm embryo the preopercular line contains but five neuromasts.

[1] That there is such a part in the *Antiarchi* is very probable, but this interpretation depends upon comparison with Arthrodires and upon the assumption that the long "oblique pit-line" in the *Antiarchi* is really homologous with the pineal line in the Arthrodires, which we do not doubt. The strict evidence should be given by the innervation which, however, can never be known. Therefore we accept the topographically acceptable interpretation of the otic part in *Antiarchi* as possible.

3. In connection with these 5 neuromasts bones develop, the bone development beginning on the frontal and caudal sides of the second and third neuromast counted from below. Then the development of bone extends to the first and to the fourth and fifth.

4. The fifth neuromast lies where the horizontal pit-line (secondary jugal line) meets the preopercular line.

5. The sixth and the seventh neuromasts of the preopercular line appear late and are present in the 15.7 mm stage as very small organs, lying dorsally to the meeting point of the preopercular line and the "horizontal pit-line". They are located caudally to the rudiment of the spiracular opening.

6. Ultimately bone rudiments appear in relation to these two dorsal organs. These rudiments join the other preopercular bone elements and in that way the preopercular bone of the adult fish is formed.

7. Thus the preopercular line in *Amia* consists of a ventral longer part and a dorsal shorter, the dorsal developing considerably later than the ventral.

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The statement in the seventh paragraph covers the conditions in *Polypterus* and *Teleosts*. In *Polypterus* there are only three neuromasts in the preopercular line and these belong to its ventral portion below the "horizontal pit-line", whereas the late developing dorsal portion has no neuromast. In Teleosts the dorsal portion may sometimes be absent and then the lower portion contains the primary neuromasts (secondarily, many times developed in great number). When the dorsal portion is present, it develops later than the ventral, just as in *Amia*. In an early embryonic stage, where vestiges of a dorsal part of the preopercular line are not present the ventral part is connected, as is the case in *Cobitis*, with the postorbital part of the infraorbital line by the rudiment of the jugal line system, (horizontal pit-line).

For determination of the equivalent of the ventral part of the preopercular line in such fishes where no dorsal part of this line is present, it is of great importance to find a landmark representing the point where the jugal line meets the ventral preopercular line. In those cases where the jugal line is represented by a normally located "horizontal pit-line" and a dorsal preopercular line portion is present, this point is well defined. But in those adult fishes where the "horizontal pit-line" is developed as a jugal canal which more or less imperceptibly passes over into the ventral preopercular canal, the limit between the canals can only very approximately be determined as located where the bend reaches its apex. Where there is no pronounced curve and no preopercular bone is developed, the limit cannot be determined at all. In embryos of recent fishes it seems generally to be possible to make the decision, as this limit may be determined by the point from which the cephalic part of the dorso-ventral lateral line issues. In Teleosts this point coincides with the point where the "horizontal pit-line" meets the ventral preopercular line. A placode from which the opercular lines of neuromasts form develops at this point, in a caudal

direction. In *Neoceratodus* (10.6—12 mm embryos) similar placodes develop, in similar location somewhat dorsal to the apex of the curve of the jugo-mandibular line. In addition to this primordium there is in the 10.6 mm *Neoceratodus* another line primordium located more ventrally on the jugo-mandibular line. This primordium is in *Protopterus* developed as the long, ventral lateral line of which at least the posterior gular line is a detached part. In *Protopterus* a counterpart of the opercular line in *Neoceratodus* develops very late and forms sometimes a short pit-line (the dorso-ventral lateral line) immediately below and in front of the gill-slit. In *Protopterus* the ventral lateral line is situated very low on the cheek. In *Chlamydoselachus* the upper end of the prospective preopercular line is marked by the post-jugal twig on the jugo-mandibular line. In the embryo of *Squalus* this same point is in the very early embryo located as a knob in flush with the horizontally extending jugal line. In *Chimaera* and *Rhinochimaera* the "ampullar line" may represent the twig in *Chlamydoselachus*.

There is, thus, in the jugo-mandibular line of primitive fishes a portion developed which answers to the lower portion of the preopercular line in higher. This portion is the more or less vertical portion of the jugo-mandibular line lying between the before mentioned "point" and the mandibular joint. In fishes where this portion is not related to any sensory line bones it is quite like the jugal line. But as soon as it becomes related to bones, it gets the character of a ventral part of the preopercular line, to which in Actinopterygians is added the dorsal part of the same line. The bones which have originated from the ventral part of the preopercular portion of the jugo-mandibular line are the preopercular bones. But also the more or less horizontally running dorsal part of the jugo-mandibular line generally develops a bone or a bone series, the squamosal. It must, however, be observed that a separate squamosal only seems to develop when the jugal line is developed as a jugal canal. When the jugal canal is developed as a pit-line, it may be reduced to an anterior process of the preopercular bone or be absent. These are questions upon which we will not enter in this paper. Yet, we must state that STENSIÖ, when considering the entire cheek portion of the jugo-mandibular line as a preopercular line, has expressed the opinion that the squamosal is an upper preopercular bone. Our statements in the preceding pages, thus, involve a rebirth of the squamosal in the head morphology of fishes.

LATERAL LINE SYSTEM IN HETEROSTRACI AND GNATHOSTOMI.

HOLMGREN (1942, 1) has made an attempt at an explanation of the gnathostomian lateral line system on the basis of agnathian conditions. This

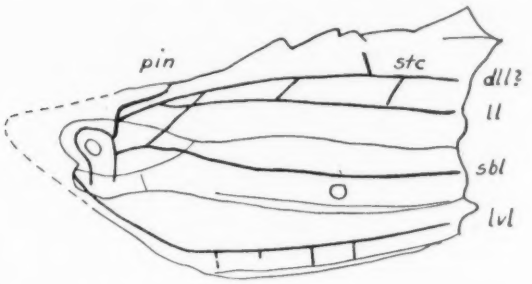

Fig. 50. *Phialaspis pococki.* According to WHITE (1946).

attempt was not successful as the evidence upon which is was based was insufficient. The description of the Heterostracan species *Phialaspis pococki* by E. I WHITE (1946) has given at least one very important piece of information which very conveniently throws light upon our problem. WHITE's description includes the discovery of a strong suprabranchial line on the branchio-cornual plate dorsally to the branchial aperture. Such a line was not known in 1942. Neither was it known at that time that a corresponding line is present in the 18 mm embryo of *Squalus* and in the embryos of *Neoceratodus* and *Protopterus* as well as in the adult *Holoptychius* and other fishes. This line is the spiracular line with the spiracular organ and post-spiracular neuromasts (*Neoceratodus* and *Protopterus*) as has been explained earlier in this paper (p. 280). It was not known, either, that there is an early apical (primary) connection between the oral and the mandibular lines in *Squalus, Dipnoi* and *Necturus.*

The suprabranchial line in *Phialaspis* undoubtedly corresponds to the suprabranchial line of neuromasts groups in *Petromyzon* and *Dipnoi.* Dorsally to the suprabranchial line there are in the branchial region of *Petromyzon* (fig. 49) two or three other longitudinal lines of which the ventral one, "the lateral line", issues caudad from the posterodorsal part of the eye whereas the dorsal line, "the dorsal lateral line", seems to be connected with the supratemporal commissure.[1] In *Phialaspis* (fig. 50) and most other *Heterostraci* the corresponding lines are present, but, they are well defined canals, connected with one another by means of transversal canals. The number of these transversal canals is somewhat varying, but, generally, they are three. In Gnathostomians also two or three longitudinal lines may be present dorsally to the spiracular line, viz. the main lateral line, and—behind the temporal commissure—the dorsal lateral line and between them the "accessory lateral line". The transversal lines which in the Pteraspids connect the longitudinal lines are, in the Gna-

[1] This dorsal lateral line further caudally divides into two lines of which the dorsal may be the real "dorsal lateral line" comparable with the "dorsal lateral line" in *Pteraspis.* The ventral then could represent the "accessory lateral line" in higher fishes (lateral line in *Pteraspis* (HOLMGREN 1942). The homologies of the lateral line system of the trunk, however, are not as yet sufficiently well established.

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thostomians, suggested to represent the supratemporal commissure, the posterior and the middle line of pits and the pineal line. In Gnathostomians, the dorsal (medial) longitudinal line is generally missing in the head part, but, in the Holocephalians, in certain Holosteans and Teleosts a similarly located longitudinal line occurs. In *Callorhynchus* it seems to be crossed by the transverse pit-lines. No decisive objections seem possible to raise against this attempt at a general, not detailed, homologisation of the dorsal line system in the *Heterostraci* and the *Gnathostomi*.

The lines on the ventral half of the head offer greater difficulties in homologising. Nevertheless, the following facts may serve as a good guide. In the Gnathostomians there exist two lines in this part, viz. the jugal and the oro-mandibular line[1] which both, in embryos of *Protopterus*, continue caudad in a direction towards the trunk, both ventrally to the gill slit.

In the Heterostraci (fig. 51) there are also two longitudinal lines on the ventral part of the head region (on the ventral plate). Of these two lines the dorsal (lateral) one is generally stronger developed than the ventral (medial) one of which the frontal part many times is differentiated from the caudal division, where it is mostly more or less broken up in almost transversely located short line divisions. The dorsal (lateral) line generally has some ventrally (mesially) directed short branches. The two ventral longitudinal lines leave the ventral plate at its anterior corner. What then becomes of the two lines is only known in a few species and seems to vary. Either they meet (fig. 51) to join the infraorbital canal—sometimes already on the ventral plate (*Poraspis siemiradzkii*)—by means of a common canal, or, they join it separately, or, they behave otherwise as seems to be the case in *Phialaspis*. Generally, however, this part of the line is unknown.

Comparing now the *Heterostraci* with the *Gnathostomians* (figs. 51 and 52) we find it very probable that the two pairs of ventral lines are homologous and that the jugal line in the Gnathostomians corresponds to the frontal part of the lateral ventral line in the Pteraspids. The mandibular part of the mandibular line in Gnathostomians corresponds to the anterior part of the medial ventral line of the Pteraspids.

Now it remains to explain how the dorsal or lateral (jugal) line of the Gnathostomians got connected with a ventral or medial (mandibular) line in the *Heterostraci*. For this purpose we are forced to make a construction. Imagine that, for instance, the foremost transversal twig on the lateral ventral line got connected with the medial line (fig. 52), and the condition could be established which we have found, earlier, in the young embryos of *Necturus*, *Neoceratodus* and *Squalus* where the oral and mandibular line placodes are connected apically. When the jaw processes were formed at the frontal part

[1] As pointed out in preceding pages (p. 307) the oral and the mandibular lines are connected frontally in young embryos.

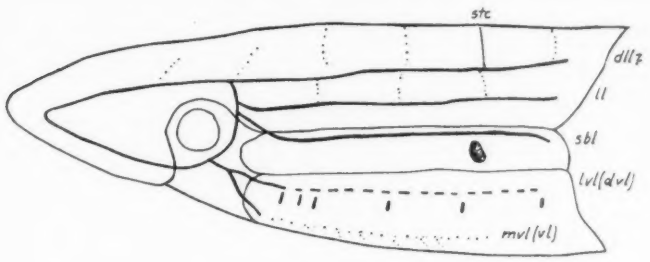

Fig. 51. Heterostracian type. General pattern. Diagram.

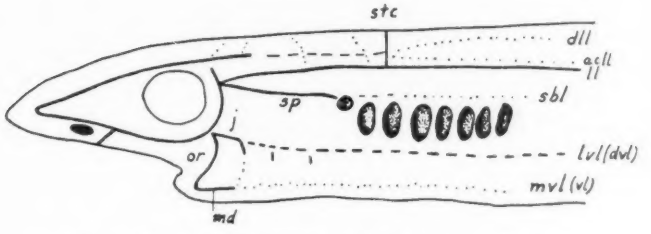

Fig. 52. Gnathostomian type. General pattern. Diagram.

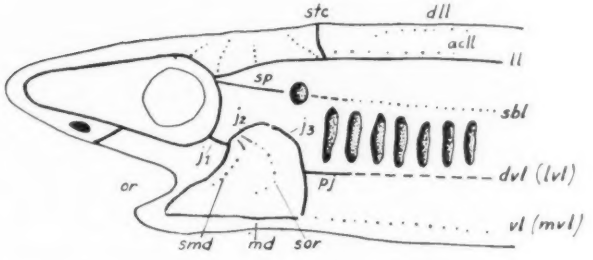

Fig. 53. Gnathostomian type. General pattern, advancing type. Diagram.

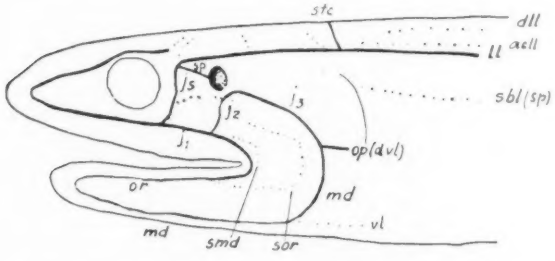

Fig. 54. Gnathostomian type. General pattern, advanced type. Diagram.

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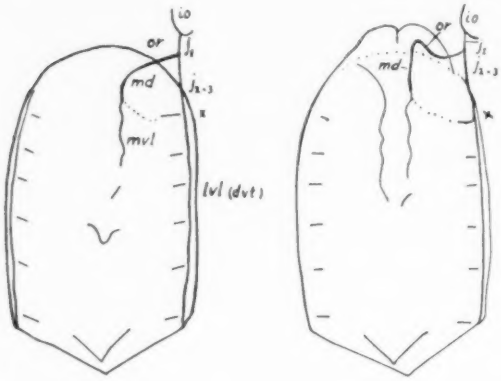

Figs. 55 A—B. Diagrams demonstrating our theory about the formation of oral and mandibular lines in Gnathostomians from Heterostracian pattern. A: Ventral shield of *Psammosteus*. B: The same with beginning mandible formation. Hypothetical junction of lateral and medial ventral lines at *x* and *x.x.*

of the ventral plate the anterior part of the medial ventral line was drawn out into this process (figs. 52, 55 A, B) and the oral and mandibular lines got their normal positions on the jaw, just as is the case in sharks, Dipnoans and the *Necturus* embryo. In Chimaeroids and sharks (and Arthrodires) the connection between the two longitudinal lines possibly has taken place far in front for instance by means of the prolongation of the foremost twig of the ventral lateral line (at *x* in fig. 55 A and B). In Dipnoans the presence of the two supernumerary pit-lines between the primary oral and mandibular lines indicate, perhaps, that the connection took place further back (fig. 53).

In this simple way the Gnathostomian conditions may be explained—as fully as preliminarily possible—from those of the Heterostracians. From this statement does not follow, however, that the Gnathostomians are derived from Heterostracians, but, only, that they may be derived from any extinct group of fishes which had a sensory line system much as in the Heterostracians. As the heterostracian sensory line system very much resembles that in *Petromyzon* the field of possible ancestral groups widens which complicates the phylogenetical questions. We do not intend to enter upon these problems.

In the pictures figs. 53 and 54 changes leading to a perfect gnathostomian type (as in *Dipnoi*) are diagrammatically represented. No detailed explanation is needed.

SUMMARY.

In this paper we have investigated the sensory lines on the cheek in fishes and amphibians in order to arrive at an interpretation of the existing different types of these lines. This interpretation is founded upon structures really present in the adult species or in their embryos. The fact that it never has been necessary to resort to extensive constructions or assumption of hypothetic lines seems to strengthen our interpretations.

The general result of this investigation is that the gnathostomian pattern is derivable from a pattern like that in the *Heterostraci*, without any farfetched assumptions or constructions.

In gnathostomian fishes two types of cheek-line systems are present. 1) One type with undifferentiated jugal line (*Holocephalia, Rajiformes, Arthrodira*) and 2) another with a differentiated jugal system (all other Gnathostomians).

The essential special results are recorded in the following table.

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	jugal 1	jugal 2	jugal 3	secondary jugal	primary oral	secondary mandibular	secondary oral	primary mandibular	opercular	primary preopercular	secondary preopercular	ventral lat. line	spiracular	Remarks
Chlamydoselachus	+	[1]+	+		+			+	[2]+	[3]+			+	[1] "middle cheek line", [2] postjugal line, [3] prospective preopercular
Squalus, embr. 18 mm	+	[1]+	+		+			+	[2]+	[3]+			+	[1] jugal line, not differentiated, [2] rudimentary, [3] prospective
Squalus, embr. 24.5 mm	+	+	+		+			+	[2]+	[3]+			[3]+	[1] rudimentary, [2] prospective, [3] spiracular organ
Squalus, adult	+		+		+			+	+	+			[2]+	[1] prospective, [2] spiracular organ
Mustelus	+		+		+			+		[1]+			[2]+	[1] prospective, [2] spiracular organ
Acanthodes	+		+		+			+						
Euthacanthus	+		+		+			+						
Neoceratodus	+	+	+	+	+	+	+	+	+	+			+	
Protopterus	+	+	+	+	+	+	+	+	+	+			+	[1] in early embryos, [2] prospective
Dipterus		+	+	+			+	+	+	+				
Holoptychius		+	+	+			+	+	+	+				
Osteolepids	[1]	+	[1]+	+	[2]		[3]+	+	+	+			+	according to our interpretation of the fossils
Chondrostei		[1]	[1]	+						[2]				[1] much reduced, [2] only on the mandible, [3] "quadratojugal" pit-line
Palaeoniscids		[1]	[1]	+						[2]				[1] in *Polyodon*, [2] possibly present, joined with the mandibular
Holostei and teleosts		+	[1]+	[2]+			[3]+	+	+	+	+			[1] reduced, [2] "horizontal pit-line", [3] "vertical pit-line"
Stegocephalia		+	[1]+	[2]+			[3]+	+	+	+	+			[1] reduced, [2] "horizontal pit-line", [3] "vertical pit-line"
Urodela		+	+	+	+		[1]+	+		+			[2]+	[1] reduced or absent
Xenopus		+	+		+		+	+	[1]+	+		+	[2]+	[1] dorsoventral lateral line, [2] only in embryo
Anura (larva)*		+	+		+		+	+	[1]+	+		+	[2]+	[1] dorsoventral lateral line, [2] only in early embryo, vestigial
Chimaeroids		+	+	[1]	+		+	+	[2]+	+		+	[3]+	[1] a special j.3., [2] dorsoventral lateral line, [3] in embryo
Rajiformes	+	+	[1]+		+			+	[2]+	[3]+			+	[1] jugal line not differentiated, [2] prospective, [3] uncertain
Arthrodira	+	+	[1]+		+			[2]+					+	[1] not differentiated, [2] drawn out caudally to meet scapular line
Antiarchi	+	+	[1]+		+								[3]+	[1] not differentiated, [2] in *Homostius*, [3] uncertain
Petromyzon	[1]+				+								[1]+	[1] not differentiated from the oral line

[1] suprabranchial line

* Non aglossal Anurans.

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ABBREVIATIONS.

acll accessory lateral body-line
al anterior pit-line
all accessory lateral line
aml "ampullar line"
apl anterior pit-line
buc buccalis-innervation
diopo postnasal dorsal branch of infraorbital line
diopr prenasal dorsal branch of infraorbital line
dll dorsal lateral line
dvl dorsoventral lateral line
extr anterior limb
g_1, g_2 gular lines
io infraorbital line
j_1 jugal 1 line
j_2 jugal 2 line
j_3 jugal 3 line
jj secondary jugal line in Anurans
js secondary jugal line
j_3+*md* jugal 3+mandibular lines
lg lateralis ganglion
ll lateral body-line
lvl lateral ventral line
md mandibular line
mdj mandibular joint
mg middle gular line
ml main lateral body-line
mpl middle pit-line
mvl medial ventral line
ol oral line
op, *opl* opercular line
or oral line
ot otic part of lateral line
pg posterior gular line
pi prepineal organs
pin pineal line
pj postjugal line (opercular line)
pl posterior pit-line
pla anterior part of the posterior pit-line
plp posterior part of the posterior pit-line
plt placodelike thickening
Po spiracular organ
pop primary preopercular line
qjl quadrato-jugal line
sb, *sbl* suprabranchial line
smd secondary mandibular line
sml secondary mandibular line
so supraorbital line
sor secondary oral line
sp spiracular line
spir spiracle
spop secondary preopercular line
stc supratemporal commissure
tl temporal portion of main lateral line
tor transversal oral line
viopo postnasal ventral branch of infraorbital line
viopr prenasal ventral branch of infraorbital line
vl ventral lateral line
xx primordium of anterior pit-line
IV glossopharyngens-innervated neuromasts
X vagus-innervated neuromasts

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ON THE CRANIAL NERVES OF THE CYCLOSTOMES WITH SPECIAL REFERENCE TO N. TRIGEMINUS

BY

THOROLF LINDSTRÖM

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I. INTRODUCTION.

Many earlier writers have tried to apply to the Cyclostomes the schema established for the cranial nerves of the Gnathostomes. The application of this schema has probably greatly increased the difficulty of making comparisons within the Cyclostome group itself. We have recently begun to get a better grasp of the systematic position and mutual relationships of the Cyclostomes. As a result of this, there is now reason for trying in the first place to compare the cranial nerves of the Myxinids and the Petromyzonids without binding oneself too strongly to a schema which can be applied to the Gnathostomes.

The present investigation deals with the trigeminal and facial nerves of the Cyclostomes and the nerves of the eye muscles of Petromyzon. Branches of the

metotic cranial nerves and of the most anterior spinal nerves are treated in so far as they are necessary for understanding the prootic nerves dealt with. Certain details of the trigeminal, facialis and spinal musculature are discussed.

JOHNSTON (1902, 1905, 1908 a) and TRETJAKOFF (1927 a, 1929 a) have considerably widened our knowledge of the cranial nerves of the Petromyzonidae. It has, therefore, been possible to write the present paper in the form of a supplement to their work. A more detailed account of the cranial nerves of Myxine is, however, given here. ALLIS's description of the nerves of Bdellostoma (1903) applies well to Myxine, but he treats only certain nerve branches. Later descriptions of the nerves of Bdellostoma differ from ALLIS's on such important points, that a new description of a Myxinid is desirable. It should be stressed once and for all that criticisms of earlier results must be taken with a certain reserve as important details in the peripheral courses of the cranial nerves appear to vary. This applies particularly to Petromyzon.

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This investigation has been carried out at the Zootomical Institute of the University of Stockholm, and I should like to express my gratitude to Professor Emeritus Nils Holmgren, the former chief of the institute, who suggested the subject. His advice regarding methods and on theoretical questions has proved indispensable to me. My thanks are also due to the present chief, Professor Torsten Pehrson, for invaluable advice and suggestions during the course of the work. I should also like to thank Professor J. LeRoy Conel, whose material, series of embryonic Bdellostoma, was put at my disposal by Professor Holmgren.

Finally, my thanks are due to Mrs. Francina Cameron for her help in translating the MS into English.

II. MATERIAL AND METHOD.

The present writer was fortunate in being able to study two sectioned embryos of Bdellostoma (Polistrotrema) stouti (dombeyi). The series belong to Professor Conel. They are stained with alum cochineal and orange G (see further p. 319 in the present paper). The author also had the privilege of studying a series from a young, 43 mm long Myxine glutinosa, belonging to Professor Emeritus Holmgren. This series is stained partly with azan-Mallory (Heidenhain) and partly with iron hematoxylin. The rest of the Myxine-material consists of 7 series of adult animals of Myxine glutinosa. These animals are fixed according to Bodian's methods 1 and 2 (ROMEIS, 1943). The thickness of a section is normally 10 μ, in some series 15 or 8 μ. The series are stained according to Bodian, PALMGREN (1948) and Rogers (ROMEIS, 1943). In addition, certain details were studied on several series of the medulla

oblongata and its immediate neighbourhood in adult Myxine. They are stained according to Cajal and Bielschowsky (Agduhr's modification, ROMEIS, 1943).

The Petromyzon-material consists of 12 series of adult Petromyzon (Lampetra) planeri and 9 series of Ammocoetes of this species and 1 series of adult Petromyzon fluviatilis. Six of the series of adult Petromyzon planeri comprise only the central part of the animal around the buccal cavity and pharynx. The total length of the Ammocoetes studied varies between 10 mm and about 5 cm. The thickness of a section is normally 10 μ in series of adults and 6 μ in series of Ammocoetes. The animals are fixed according to Bodian's method 2 and Bouin's method and stained according to Bodian and Palmgren. In addition, some series are fixed and stained according to Bielschowsky (Agduhr's and Boeke's modifications, ROMEIS, 1943). Only the main features of the cranial nerves could be studied in the smallest Ammocoetes specimens. Details given in the present paper refer to Ammocoetes specimens longer than 25 mm.

Moreover, the author has had access to series of Myxine, Ammocoetes and adult Petromyzon (one specimen) belonging to the Zootomical Institute. The adult specimen of Petromyzon was caught in the Fyris (a river flowing into Lake Mälar). For the systematic position of this specimen, the reader is referred to ENEQUIST (1937, p. 5).

All reconstructions are graphical, based on photographic negatives of the sections. Some of the illustrations are mirror images of the originals.

Fixatives containing formaline were used in order to achieve as complete a silver impregnation as possible. This led to certain difficulties in sectioning and to defects which could not be avoided. The Cyclostomes, particularly Petromyzon, are characterized by a certain variation in the branching and course of the cranial nerves (Chapter VIII). It is, therefore, possible that the nerves may have had aberrant courses in areas damaged in sectioning, so that the present material would then give only an imperfect picture of the nervous system of Petromyzon. The study of a greater number of series would eliminate these deficiencies, but the author has preferred instead to pay special attention to the character of the variation (Chapter VIII).

Bodian's and Palmgren's methods result in a very distinct impregnation of nerve fibres, which is a great advantage when one is trying to separate intersecting branches or branches joined together into one bundle.

As a rule it was impossible to trace the nerves to the free endings or to the end organs in muscles, skin, mucous membranes, etc. As the various nerve branches are not clearly defined in character, it would be more correct not to use the terms "motor" and "sensory" nerve branches. In the descriptive part of this paper, however, the term "motor" is used of branches which terminate in muscles and "sensory" of branches terminating in skin or mucous membranes. This question will be discussed in chapter XII:3 D.

III. NOMENCLATURE.

HOLMGREN—STENSIÖ's skeletal nomenclature (1936) will be used with the modifications made by HOLMGREN (1946) and JOHNELS (1948). COLE (1908) gave an excellent description of the musculature of Myxine. The names of the muscles were, however, changed by LUTHER (1938), and it is the names used by the latter, which will be used here as they are more in line with modern skeletology. Lists of synonyms of the muscles may be found in COLE's and LUTHER's works. TRETJAKOFF's nomenclature for the musculature of Petromyzon (1926 a, 1929 a) has been partly modified by DAMAS (1935) again to bring it more in line with modern skeletology. DAMAS' modification will be used here, particularly as his description of some of the muscles in the Ammocoetes fit the present material better than TRETJAKOFF's (1929 a). Lists of synonyms are to be found in TRETJAKOFF's and DAMAS' works.

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The nomenclature of the cranial nerves of the Myxinidae is partly compiled from earlier writers and partly new. In order to facilitate comparison with previous literature on the subject references will be given to P. FÜRBRINGER (1875). TRETJAKOFF's nomenclature for the nervous system of Petromyzon (1927 a) will be followed as closely as possible.

IV. TWO EMBRYONIC STAGES OF BDELLOSTOMA.

These stages illustrate the development of some cranial nerves of the Myxinids and the relationship between the muscle groups in embryonic Myxine (HOLMGREN, 1946) and the muscle system of an adult Myxinid. There are very few differences between the muscle systems of the adult Myxine and the adult Bdellostoma. This is most clearly shown by the fact that the writers describing the relationship between nerves and muscles in Bdellostoma, do not take as their starting point the latest description of the musculature of Bdellostoma (MÜLLER, 1836), but P. FÜRBRINGER's (1875) description and nomenclature relating to Myxine.

The embryos studied are those which CONEL (1929) called No. 2266 and No. 1. CONEL writes of No. 1, which is the elder: "The embryo had probably hatched a very short time before it was found". In the present paper only those tissue areas are described as muscle primordia where a more or less far advanced formation of muscle fibres could be observed. No attention has been paid to the development of the connective tissue apparatus of the muscles. When it is stated that a muscle primordium has "reached" or "made contact with" a cartilage, this does not mean that the muscle fibres are directly attached to the cartilage but that the extension of the connective tissue, uniting the

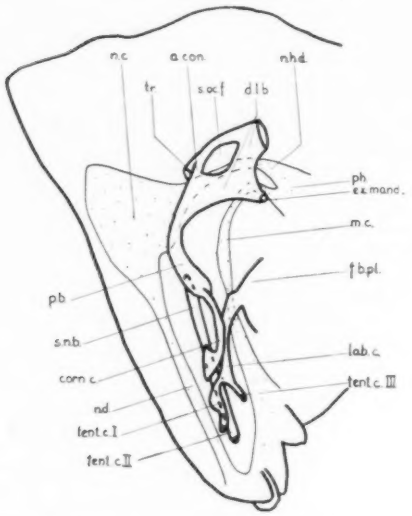

Fig. 1. Bdellostoma embryo, stage I. Reconstruction of some main structures of the head. Lateral view. 25 ×.

muscle fibres and the cartilage, is insignificant. Data regarding position refer to the actual position in the embryo. The term "rostral" ("rostrad")—which is the only one that can possibly lead to any confusion—implies a situation (direction) opposite to "caudal" ("caudad").

1. STAGE I.

The snout points ventrad, at a right angle to its position in the adult animal. The skeleton is well-developed. The cornual cartilage, subnasal cartilage, labial and tentacle cartilages, the nasal duct and the anterior part of the dorsal longitudinal bar lie chiefly dorso-ventrally (fig. 1). The trabecles continue towards the nasal capsule as in the embryonic Myxine described by HOLMGREN (1946). They are not bent at the angle, so characteristic of the trabecles in the adult Myxinids.

A. The Musculature.

The grouping of the trigeminal and facialis musculature is in accordance with HOLMGREN'S (1946) description. The buccalis group consists of two muscle primordia lateral to r. externus, and a large number of primordia medial to the nerve. Of the lateral primordia (fig. 2), m. levator cartilaginis basalis (*m.l.c.b.*) lies somewhat isolated from the rest of the buccalis group and in close contact with mm. protractores cartilaginis basalis (*m.p.c.b.a.,p.*) with

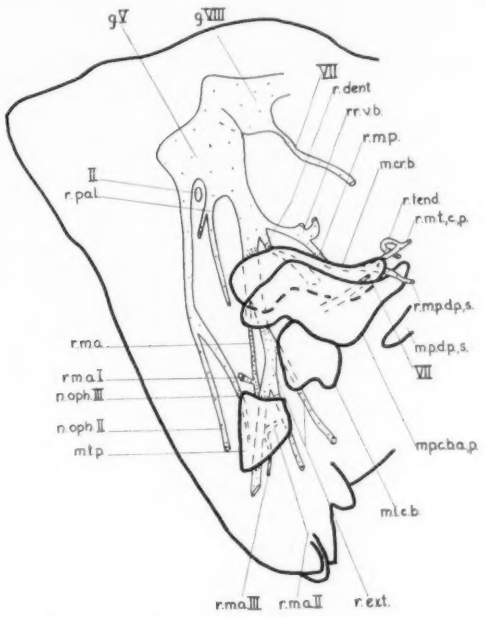

Fig. 2. Bdellostoma embryo, stage I. Reconstruction of n. trigeminus, n. facialis and the lateral muscle primordia belonging to the trigeminal and facialis musculature. N. facialis is incomplete in the reconstruction. Lateral view. 28 ×.

which it later collaborates. M. levator cartilaginis basalis lies lateral to the frontal basal plates. The other muscle primordium in the lateral group is m. tentacularis posterior (*m.t.p.*). The extension of this primordium is considerably more limited relative to the surrounding structures than is that of the developed muscle. The muscle primordium covers approximately the place where the labial cartilage divides into two branches.

The medial buccalis group (fig. 3) consists of two isolated primordia and a group primordia in which it is not easy to differentiate the separate muscles. The isolated primordia are m. nasalis (*m.nas.*) lying lateral to the nasal duct and m. coronarius (*m.cor.*) lying dorso-rostral to the basal part of the tentacle cartilage I. In the combined group of muscles may be seen m. trabeculo-subnasalis superficialis (*m.tr.s.n.s.*), which stretches between "the palatine bar" and the subnasal cartilage. The primordium of m. trabeculo-subnasalis profundus (*m.tr.s.n.p.*) stretches from "the palatine bar" and the cornual cartilage to its origin close to the insertion of m. trabeculo-subnasalis superficialis in the subnasal cartilage. A connecting region for the whole group of muscles lies near the subnasal cartilage. From here the primordium of m. subnasali-basalis (*m.s.n.b.*) stretches caudo-dorsad towards the anterior edge of the frontal basal plates. Another, more ventral primordium also stretches caudo-dorsad from the

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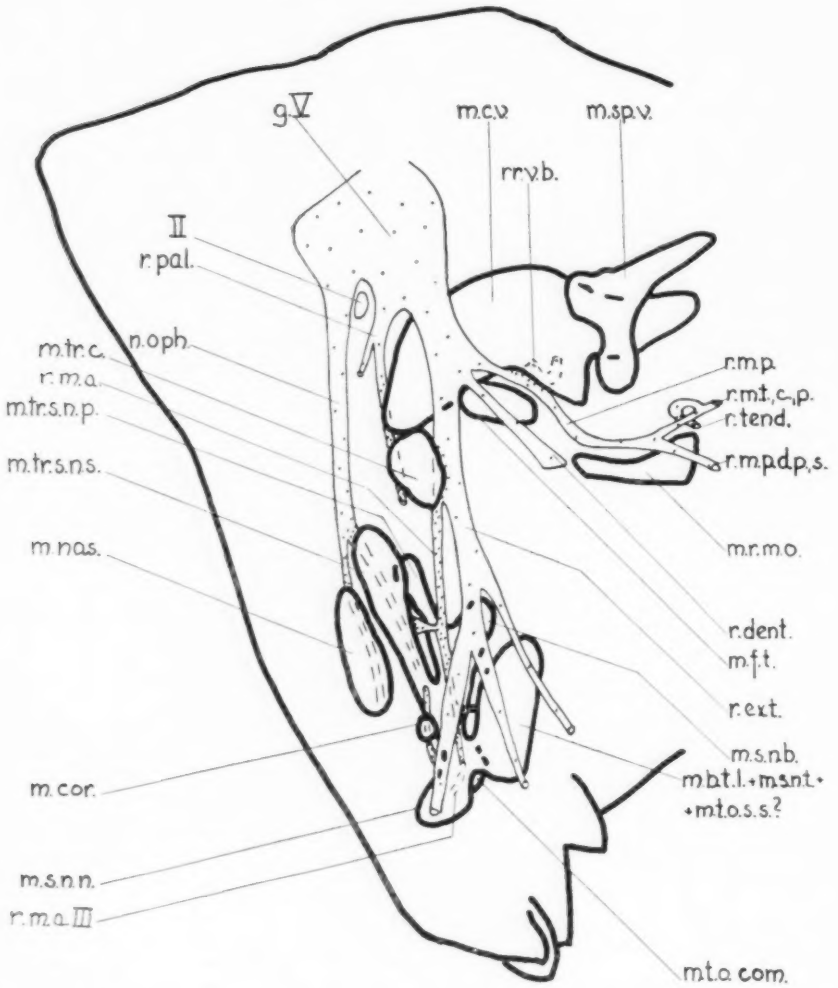

Fig. 3. Bdellostoma embryo, stage I. Reconstruction of n. trigeminus and the medial muscle primordia. Lateral view. 50 ×.

connecting region, groups itself around the tentacle cartilage III, leaving the lateral surface of the cartilage free, and terminates near the anterior edge of the frontal basal plates. This primordium contains m. subnasali-tentacularis (*m.s.n.t.*), m. basali-tentaculo-labialis (*m.b.t.l.*) and parts of m. transversus oris (*?m.t.o.s.s.?*). The existence of a connecting region for the group of muscles near the subnasal cartilage does not imply that m. basali-tentaculo-labialis, for example, actually reaches the cartilage, but that it cannot be separated from others that do. Finally, a group consisting of two primordia originates in the

connecting region. One (*m.t.o.com.*) is the ventral commissure of m. transversus oris (COLE, 1908), which passes caudal to the base of the tentacle cartilage II and joins the corresponding primordium from the other half of the body at a point caudal to the nasal duct and rostral to the mouth opening. The other primordium is m. subnasali-nasalis (*m.s.n.n.*) which stretches, dorsal to the tentacle cartilage II, up to the nasal duct.

The velar group consists of a primordium lateral to the V_2-nerves and a group primordia lying wholly or partly medial to these nerves. The lateral primordium is m. cranio-basalis (fig. 2, *m.cr.b.*). It occupies the space between the extra-mandibular, the part of the dorsal longitudinal bar which forms the ventral boundary of the subocular fenestra, and the lateral edge of the frontal and the medium paired basal plates. Among the medial primordia (fig. 3) m. trabeculo-coronarius (*m.tr.c.*) lies in the angle between the part of the dorsal longitudinal bar which forms the ventral boundary of the subocular fenestra and the downward bent "palatine bar". The muscle is not connected to the skeletal bars. The primordium of m. flexor trabeculae (*m.f.t.*) lies along the ventral edge of the extra-mandibular. In the space between the buccal cavity and the pharyngeal basket lie the primordia of m. craniovelaris (*m.c.v.*) and m. spinovelaris (*m.sp.v.*). The former primordium encircles the head of the velar cartilage and stretches caudad along the medial side of the cartilage. The primordium of m. spinovelaris lies dorso-lateral to the head of the velar cartilage and stretches caudad from there under the base of the cranium to the neighbourhood of the notochord.

The primordium of m. retractor mucosae oris (fig. 3, *m.r.m.o.*) lies isolated and it is uncertain in which group to include it. It is not in immediate contact with the wall of the buccal cavity.

The primordia of mm. protractores dentium (ventral to the basal plates) and the pharyngeal roll could be observed, but will not be described.

The primordia of mm. protractores cartilaginis basalis (fig. 2, *m.p.c.b.a.,p.*) occupy a considerably more rostral position than they do in the Myxine embryo described by HOLMGREN (1946). They lie in the same transverse region as the buccalis and the velar groups and cover the space between the extra-mandibular and the lateral edges of the frontal and the medium paired basal plates, lateral to the primordium of m. cranio-basalis.

B. The Nerves.

It was not possible with the present material to investigate satisfactorily the details of the ganglia of the trigeminal-facial group. The motor root could not be delimited in the trigeminal complex. No cutaneous branch of n. ophthalmicus could be observed near the eye. On the other hand, the two branches,

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which in the adult Myxine are called the dorsal and the ventral trunks of the ophthalmicus, were found. The "dorsal" one (rostral in the embryo, fig. 2, *n.oph.II*) runs along the nasal duct, medial to m. nasalis. The "ventral" one (caudal in the embryo, *n.oph.III*, cf. fig. 3) cuts through the primordium of m. trabeculo-subnasalis superficialis and divides into two branches, one on either side of the base of the tentacle cartilage II. R. palatinus (fig. 3, *r.pal.*) runs rostral to the anterior connection between the trabecle and the dorsal longitudinal bar, caudal to n. opticus and lateral to the trabecle. One branch of the palatinus runs towards the nasal duct, and another runs ventrad in the roof of the buccal cavity and is lost near "the palatine bar". All other branches of the trigeminus pass through the subocular fenestra. R. externus (fig. 3, *r.ext.*) has three branches running to the tentacles I, III and IV, lateral to the labial cartilage and the tentacle cartilages I and III but caudal to the cornual cartilage. The branch to tentacle I may possibly be said to run somewhat medial to the cornual cartilage. Proximally, r. muscularis anterior (figs. 2, 3, *r.m.a.*) cannot be described as an isolated nerve; it is united with r. externus into a joint trunk. R. muscularis anterior runs medial to the caudal part of m. trabeculo-coronarius and medial to both the labial cartilage and the cornual cartilage—except for the basal part of the cornual cartilage. The branches of the nerve and their courses could not be conclusively disentangled by the author. A branch is, however, given off when the nerve passes medial to the cornual cartilage. This branch runs rostrad (*r.m.a.I*) and links up with m. trabeculo-subnasalis superficialis and profundus. Another branch is given off from the motor nerve medial to the ramification point of the labial cartilage (*r.m.a.II*). This nerve runs caudad towards the m. basali-tentaculo-labialis complex. Further ventrally, m. coronarius probably receives a nerve bundle from r. muscularis anterior. This branch runs rostral to the labial cartilage. The rest of r. muscularis anterior (*r.m.a.III*) runs to the complex consisting of m. subnasali-nasalis and the commissure of m. transversus oris. R. dentalis (figs. 2 and 3, *r.dent.*) runs lateral to m. flexor trabeculae, medial to m. cranio-basalis and rostral to m. retractor mucosae oris and reaches the dental plate. R. muscularis posterior (figs. 2, 3, *r.m.p.*) cannot be delimited proximally from a sensory nerve to the mucous membrane of the buccal cavity. This sensory nerve (*rr.v.b.*) turns off, however, mediad between m. flexor trabeculae and m. craniovelaris and reaches the dorsal wall of the buccal cavity near the orifice of the naso-hypophysial duct. R. muscularis posterior continues caudad and runs caudal to m. flexor trabeculae, medial to the extra-mandibular and dorsal to m. retractor mucosae oris, and gives off r. mm. protractores dentium (*r.m.p.d.p.,s.*). This branch makes its way out laterad, dorsal to m. retractor mucosae oris and between m. cranio-basalis and mm. protractores cartilaginis basalis. Further caudally, r. muscularis posterior gives off yet another branch

which describes a loop and enters the tendon of m. clavatus (*r.tend.*). The main trunk of r. muscularis posterior runs to the pharyngeal roll.

N. facialis (fig. 2, *VII*) can be traced in this specimen peripherally up to a point immediately proximal to that at which the nerve is supposed to pass behind the extra-hyal. Peripherally to this it cannot be traced until it reaches a position lateral to m. cranio-basalis. From here it can again be traced distad, lateral to the primordium af the said muscle and medial to mm. protractores cartilaginis basalis.

2. STAGE II.

At this stage the process, which results in the ventrally-pointed snout of the embryo pointing rostrally in the adult animal, has begun.

A. The Musculature.

In the buccalis group the primordium of m. tentacularis posterior (fig. 4, *m.t.p.*) has extended little in relation to the surrounding structures. The primordium of m. levator cartilaginis basalis (*m.l.c.b.*) still does not reach as far as the cornual cartilage. The primordia of m. trabeculo-subnasalis superficialis and profundus (fig. 5, *m.tr.s.n.s.*, *m.tr.s.n.p.*) are better separated close to the subnasal cartilage than they were in the previous stage. M. trabeculo-subnasalis superficialis is inserted ventral to the origin of the other muscle. Still more ventral, the primordium of m. subnasali-basalis (*m.s.n.b.*) has its origin on the subnasal cartilage and stretches dorso-caudad up to the anterior edge of the lateral frontal basal plate. Three primordia have a common origin on the subnasal cartilage, ventral to the previous primordium and dorsal to the point at which the cartilage gives off the tentacle cartilage II. M. subnasali-nasalis (*m.s.n.n.*) stretches rostrad to the nasal duct and m. subnasali-tentacularis (*m.s.n.t.*) + m. transversus oris sensu stricto (*m.t.o.s.s.*) (Cole, 1908) run caudad and laterad to a position ventral and caudal to the tentacle cartilage I. Here, the two primordia join m. basali-tentaculo-labialis (*m.b.t.l.* The primordia *m.b.t.l.*, *m.s.n.t.* and *m.t.o.s.s.* are not separated in the figure.). The medial commissure of m. transversus oris (*m.t.o.com.*) has detached itself from the rest of the primordia and forms a transverse commissure across the median line, caudal to the tentacle cartilage II and rostral to the mouth opening. The primordium of m. basali-tentaculo-labialis stretches mainly caudad from its point of connection with m. subnasali-tentacularis and m. transversus oris sensu stricto, running on the medial side of tentacle cartilage III, and reaches the lateral frontal basal plate somewhat caudal to the insertion of m. subnasali-basalis. Caudal and lateral to the labial cartilage, a process from m. basali-tentaculo-labialis joins m. coronarius (*m.cor.*). No change worth pointing out has taken place in m. nasalis.

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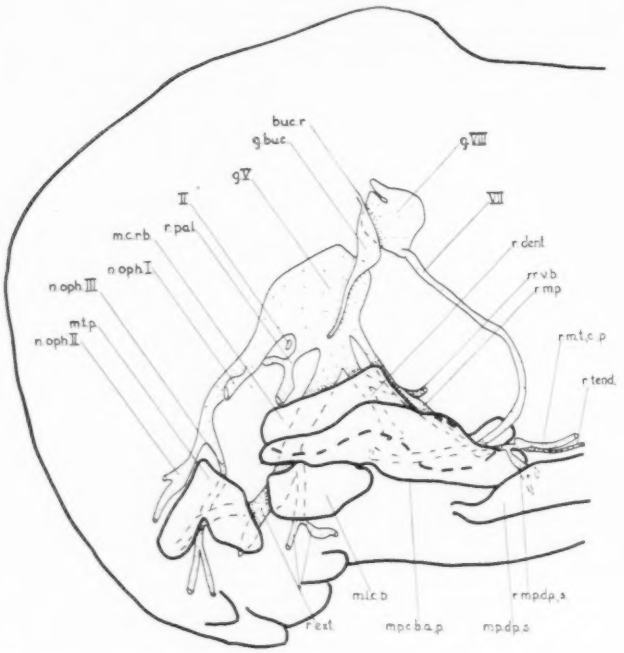

Fig. 4. Bdellostoma embryo, stage II. Reconstruction of n. trigeminus, n. facialis, the acoustic ganglion and the lateral muscle primordia belonging to the trigeminal and facialis musculature. Lateral view. 25 ×.

In the velar group, m. cranio-basalis (fig. 4, *m.c.r.b.*) reaches as far as the extra-mandibular and the lateral frontal basal plate and is in contact with both. The primordium does not appear to stretch as far as the lateral edge of the medium paired basal plates. M. trabeculo-coronarius (fig. 5, *m.tr.c.*) has not yet achieved contact with either the dorsal longitudinal bar or the labial cartilage, and lies medial to both r. externus and r. muscularis anterior. M. spino-velaris (*m.sp.v.*) has achieved contact with the chordal sheath caudal to the parachordalia. M. retractor mucosae oris (*m.r.m.o.*) lies closer to the wall of the buccal cavity than at the previous stage.

In the hyoid group, mm. protractores cartilaginis basalis (fig. 4, *m.p.c.b.a.,p.*) makes contact with the extra-mandibular, the lateral frontal basal plate and the medium paired basal plates.

B. The Nerves.

A motor root isolated from the rest of the trigeminal complex could not be identified at this stage either. N. ophthalmicus gives off a branch to the skin ventro-rostral to the eye (fig. 4, *n.oph.I*). The caudal trunk of the ophthalmicus

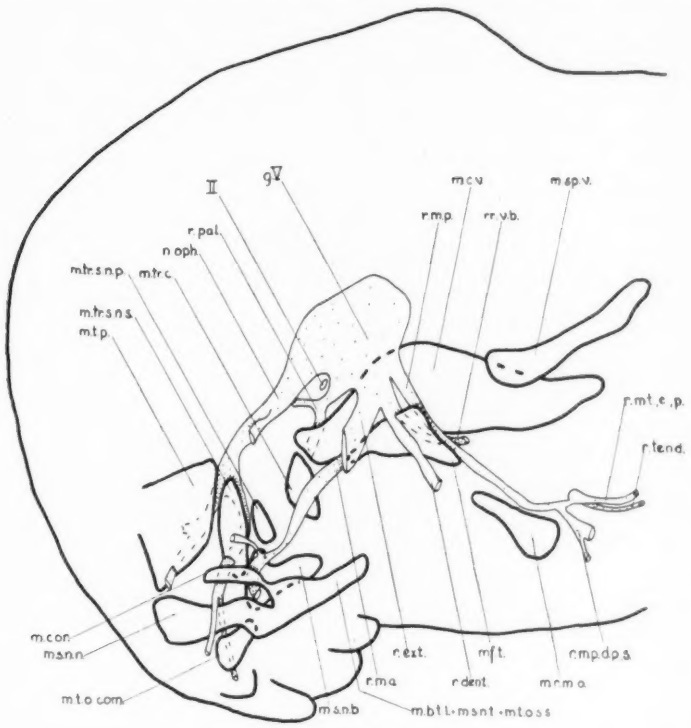

Fig. 5. Bdellostoma embryo, stage II. Reconstruction of n. trigeminus and the medial muscle primordia. Lateral view. 28 ×.

(*n.oph.III*) runs between m. trabeculo-subnasalis superficialis and profundus, and cuts through m. trabeculo-subnasalis superficialis further distally, as in the previous stage. Further distally, the nerve sends off two branches which run rostral to the base of the tentacle cartilage II. These branches pierce the ventral commissure of m. transversus oris and are lost in the skin rostral to the mouth opening. The rest of the caudal trunk of the ophthalmicus is destined for tentacle II. No important changes have taken place in the course of the rostral trunk of the ophthalmicus (*n.oph.II*). A branch of r. palatinus can be traced rostrad to the ventro-medial surface of n. ophthalmicus, but further distally the two nerves cannot be distinguished. Another palatinus branch runs ventrad between the trabecle and the dorsal longitudinal bar, rostral to the anterior connection between these skeletal bars. The branch divides into a rostral and a caudal branch, which are lost a little further distally in the neighbourhood of the buccal cavity and the naso-hypophysial duct respectively. That is to say, the rostral branch cannot be traced as far as at the previous stage. This is probably due to differences in staining between the two specimens.

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A change, as compared with the previous stage, may be observed in the branch of r. externus to tentacle I—it lies for a short distance clearly medial to the cornual cartilage. The most caudal of the branches of r. externus runs between m. levator cartilaginis basalis (laterally) and m. subnasali-basalis and m. basali-tentaculo-labialis (both medially), and divides into two end branches: one to tentacle IV and one to the skin caudal to the tentacle. No important changes in the course of r. muscularis anterior (fig. 5, *r.m.a.*) could be observed at this stage. Only fragments of the branch to m. subnasali-nasalis and the commissure of m. transversus oris could be observed. M. coronarius receives a branch running caudal to the labial cartilage and probably another rostral to the cartilage. The small, sensory nerve to the wall of the buccal cavity (*rr.v.b.*), which in the previous stage was joined proximally to r. muscularis posterior, is now joined proximally to r. dentalis (*r.dent.*). The loop described by the nerve to the tendon of m. clavatus (*r.tend.*) is less marked at this stage.

A buccalis nerve can be observed. Its root lies dorsal to the acoustic ganglion and its ganglion lies lateral to both the acoustic and the trigeminal ganglia. The nerve runs to the skin ventro-caudal to the eye. The facial nerve can be traced without interruption in this specimen. It emerges from the ventral edge of the acoustic ganglion. The root cannot be traced in its course through the ganglion. It is impossible to decide whether a facial ganglion exists or not.

3. DISCUSSION.

The connection between the muscle primordia in these stages of Bdellostoma and the muscle groups in the Myxine embryo described by HOLMGREN (1946) appears to be clear as far as the main features are concerned. However, a number of primordia are possibly missing in HOLMGREN's embryo. It is chiefly the lateral primordia which cannot be identified, e.g. m. tentacularis posterior, m. levator cartilaginis basalis and m. cranio-basalis. It remains to decide by studying intermediate stages whether these muscle primordia are developed independently on the place where they are found at older stages or whether they are formed as the result of splitting off from the primordia described by HOLMGREN. As far as the velar group is concerned, the former alternative seems most likely. Some stages, older than stage II in the present material, would also appear to be necessary for clarifying completely the development of, for example, m. transversus oris. In the main, however, the mutual positions of the muscle primordia, nerves and skeletal elements in the stages described correspond to the conditions in the adult animal, provided we make the reservation that the snout turns through an angle of 90°.

The size of the muscles, however, must be considerably enlarged relative to the other structures in the head before the adult conditions are achieved. This enlargement seems to be less marked in the case of m. craniovelaris and m.

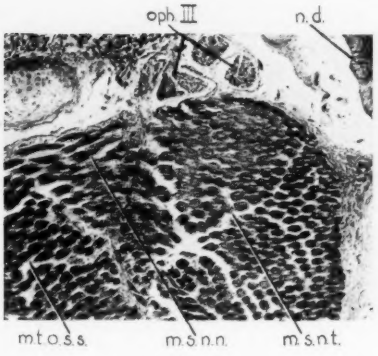

Fig. 6.

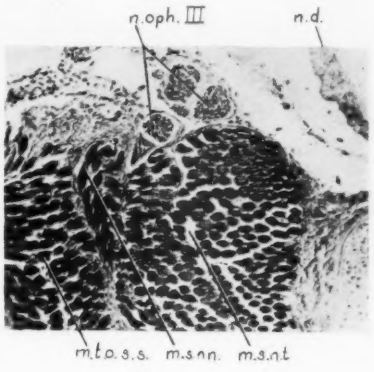

Fig. 7.

Figs. 6 and 7. Myxine, adult. Two transverse sections, separated by nine sections. In fig. 6 —the caudal section—the origin of m. subnasali-nasalis is joined to m. transversus oris sensu stricto, in fig. 7 it is joined to m. subnasali-tentacularis. 85 ×.

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spinovelaris than with the other trigeminal muscles—cf. fig. 5 with MÜLLER's (1836), P. FÜRBRINGER's (1875) or COLE's (1908) pictures of adult Myxinids. This can be linked up with the special, histologic structure of the velar musculature (COLE) or with the fact that changes in shape are not so very comprehensive inside the pharyngeal basket during the period between the stages described here and the adult stage. M. flexor trabeculae in the stages described lies along its entire length medial to r. externus and r. dentalis, and does not stretch as far rostrad as to r. muscularis anterior. In order to reach the adult state it must expand laterad and extend itself rostrad. In so doing, it is clear that in some specimens the muscle surrounds r. dentalis (p. 344). In the adult, the rostral part of the muscle runs ventral to r. externus, r. muscularis anterior and m. trabeculo-coronarius, and is inserted by means of a long tendon in "the palatine bar". This situation is indicated in the older embryo by the rostral part of the muscle primordium which tapers. M. trabeculo-coronarius lies partly lateral to r. muscularis anterior in stage I, but in stage II wholly medial to the nerve—a change that is difficult to interpret. In the adult the nerve lies completely embedded in the muscle. M. subnasali-nasalis, m. subnasali-tentacularis and m. transversus oris sensu stricto (COLE, 1908) all belong to the large, combined buccalis group in stage I. In stage II they are still joined to one another, but are relatively isolated from other muscle primordia (except m. basali-tentaculo-labialis). In the adult Myxine m. subnasali-nasalis, m. subnasali-tentacularis and m. transversus oris sensu stricto are joined up together in a small common region, so that they appear there to be fractions of one and the same muscle. COLE (1908) considers—though with some reservation—that the muscles are independent. As may be seen from figs. 6 and 7 the caudal origin of m. subnasali-nasalis (*m.s.n.n.*) in adult Myxine consists of a muscle bundle, which is joined to muscle fibres in both

m. subnasali-tentacularis (*m.s.n.t.*) and m. transversus oris sensu stricto (*m.t.o.s.s.*).

R. muscularis anterior runs in the present embryonic stages medial to both the cornual cartilage and the labial cartilage—if we exclude the short, basal part of the cornual cartilage lying in the transverse plane. If the innervation of m. coronarius has been correctly observed, then the innervation is a proof of the fundamentally medial position of r. muscularis anterior in relation to the labial cartilage, as the branches to m. coronarius run one on each side of the cartilage out to m. coronarius. M. coronarius lies lateral to the cartilage. R. externus lies lateral to the labial and the tentacle cartilages and chiefly caudal to the cornual cartilage. The branch nearest the cornual cartilage—r. tentaculi I—undergoes, however, a displacement mediad during the development from stage I to stage II. In stage II the nerve branch lies medial to the cartilage.

It has proved necessary to a certain extent in this investigation to describe the motor and sensory nerves of the trigeminus during their proximal course as joint, mixed trunks. The motor root could not be delimited. As the series are not stained so as to bring out nerve fibres, the fact that the motor root cannot be delimited does not in any way imply that the motor component does not exist as an individual bundle from the root to the peripheral branches. The course and type of ramification of the trigeminus—in so far as they could be observed in the embryonic stages—agree with the condition in the adult Myxine. These observations are not, however, sufficient to make the author able to decide which of the previous investigations of Bdellostoma are correct regarding the details of the innervation of the musculature. The agreement between the courses of the sensory branches in the Bdellostoma embryos and in adult Myxine can be proved in greater detail. The only case in which a difference could be observed concerning the courses of the sensory nerves in the Bdellostoma embryos and those in adult Myxine lies in the relationship between the ventral (in the embryo caudal) trunk of the ophthalmicus and the base of the tentacle cartilage II (see p. 327). In this case the author's observations on Bdellostoma embryo agree with ALLIS's data (1903) on adult Bdellostoma. It is the only place in which the present author's observations on adult Myxine differ from ALLIS's on adult Bdellostoma, a fact which may be taken as a criterion of the similarity between the trigeminal nerve in Myxine and Bdellostoma.

The root of n. buccalis in stage II (fig. 4, *buc.r.*) emerges from the brain further dorsally than the roots of the trigeminus and the buccalis ganglion is situated laterally (*g.buc.*). In this the buccalis agrees so obviously with ganglion C_1 and the nerve belonging to it in v. KUPFFER's (1893—1900) embryo E VIII (younger then stage II), that one must agree with ALLIS (1903) who identifies the buccalis with C_1. The buccalis ganglion lies in stage II with its caudal part

lateral to the rostral part of the next ganglion. This next ganglion has hitherto been called the "acoustic" ganglion in the present paper. The same relationship holds between ganglion C_1 and C_2 in v. KUPFFER's stage E VIII as between the buccalis and the "acoustic" ganglion at stage II. No facial ganglion could be found in the present embryonic stages, but the limited thickness of the facial nerve alone is enough to render it unlikely that any greater part of the "acoustic" ganglion represents an incorporated facial ganglion. v. KUPFFER, however, interpreted the C_2 ganglion in embryo E VIII as a facial ganglion. This would imply that the embryonic facial ganglion is considerably larger relative to the other cranial ganglia than it is in the adult, which in itself is not unlikely. It would also imply that the utricular and saccular ganglia, which are well separated in the adult are represented in v. KUPFFER's stage E VIII by only one ganglion—even if it is somewhat indented. Finally, it would imply that the facial complex is considerably displaced during the development from the stage E VIII to the adult animal, because in adult Myxinids the roots of the facialis run out through the caudal part of the utricular ganglion. NEUMAYER (1938) describes a facial-acoustic ganglion complex in embryonic Bdellostoma, in which he does not separate the ganglia from each other. N. facialis emerges from the ventral surface of the complex. Moreover, he describes an independent ganglion which should correspond to v. KUPFFER's epibranchial ganglion 6. This lies in the peripheral course of n. facialis, ventral to the auditory capsule. HOLMGREN (1946) describes separate utricular and saccular ganglia and a n. facialis emerging between them in embryonic Myxine. Moreover, HOLMGREN describes "a fingerlike ... prolongation of the mandibular ganglion", which he interprets as the facial ganglion. It presumably represents the buccalis ganglion.

v. KUPFFER is thus the only writer in whose description the position of the facial nerve relative to the acoustic ganglia differs in the embryo from that in the adult. v. KUPFFER's stage E VIII is an early one, it is true, but not earlier than NEUMAYER's youngest stage. No Myxinid embryo, hitherto described, can be said to be an intermediate stage between stage E VIII in the interpretation of v. KUPFFER and an adult animal. v. KUPFFER's interpretation certainly fits in better with the system he establishes for all the ganglia in the head, but the system is not up to date. The present writer considers it probable that ganglion C_2 and D_1+D_2 in v. KUPFFER's description represent the utricular and the saccular ganglion. In the present material it is not possible to separate the two ganglia completely (fig. 4).

How the facial ganglion (ganglia) develops is less clear. The existence of an epibranchial facial ganglion has been confirmed both by v. KUPFFER and by NEUMAYER, but could not be observed in the present material. Finally, one must bear in mind the possibility that part of the acoustic ganglion complex may represent an incorporated facial ganglion.

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V. MYXINE.

1. N. TRIGEMINUS.

The trigeminus consists of three main parts. They are, however, not the same three parts as in higher Vertebrates, but a V_1 or ophthalmic ganglion with a sensory nerve, a V_2 ganglion with also sensory nerves, and finally a motor trunk, which emerges from the brain ventro-caudal to the sensory roots and passes on the ventral side of the ganglia without any interchange of fibres taking place between it and the ganglia (fig. 8). The two ganglion elements lie partly so close together that a boundary cannot be drawn between them. The motor root contains no extra-cerebral cell bodies. NEUMAYER's "recurrens trigeminus" and "recurrens facialis" (1938, p. 185) could not be found. NEUMAYER probably interpreted the spinal nerves running rostrad as r. recurrens in both Myxine and Bdellostoma (cf. figs. 17, 20).

Since some nerve branches undergo changes in both direction and position, depending on whether the dental plate is pushed forwards or drawn back, it should be pointed out that the following description refers to specimens in which the dental plate is drawn back.

A. N. Ophthalmicus (V_1).

P. FÜRBRINGER (1875) considers that n. buccalis and the dorsal trunk of r. palatinus belong to n. ophthalmicus. The present author does not share this view. In FÜRBRINGER's nomenclature, n. buccalis and the branch of the palatinus are called: "r. cutan. sup. post." and "r. nasalis" of the ophthalmicus.

The ophthalmic ganglion lies rostrally and dorsally in the trigeminal ganglion complex. Dorsal to the anterior connection between the trabecle and the dorsal longitudinal bar the ganglion changes into a nerve running rostrad between the brain capsule and the most dorsal part of m. cranio-basalis. According to MÜLLER (1839) and P. FÜRBRINGER, n. opticus runs dorsal to n. ophthalmicus, but this mistake has been corrected by RETZIUS (1881). The eye, on the other hand, lies dorsal to n. ophthalmicus as n. opticus, although it certainly passes ventral to the ophthalmic nerve, bends off dorsad, lateral to the ophthalmicus and only reaches the eye more peripherally. Immediately rostral to the intersection of the opticus and the ophthalmicus, the latter gives off a branch called by FÜRBRINGER "r. cutan. sup. ant." The branch (fig. 9, *n.oph.1*) runs laterad, rostral to the opticus and dorsal to m. cranio-basalis, describes a loop, first caudad, then rostrad, pierces m. tentacularis posterior and then runs in a rostral and somewhat lateral course to the subcutis, where it spreads out like a fan.

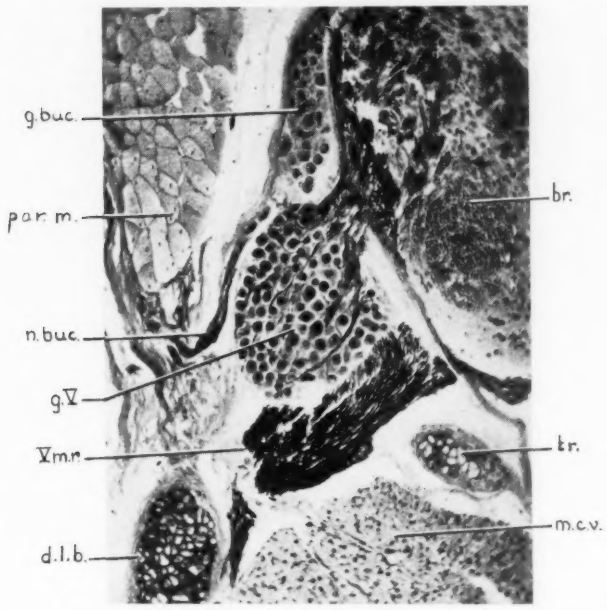

Fig. 8. Myxine, adult. Transverse section through the buccalis and trigeminal ganglia and the motor trigeminal root. 95 ×.

The main trunk of n. ophthalmicus continues rostrad and is surrounded by the following structures: the rudimentary eye dorsally, the brain capsule and the nasal capsule medially, the dorsal longitudinal bar ventrally and m. trabeculo-subnasalis superficialis laterally. In this region the dorsal trunk of r. palatinus (fig. 10, *r.pal.I*) runs close to the medial side of the ophthalmicus (p. 337). In certain specimens a small bundle detaches itself here from the ophthalmicus, runs rostrad in a more dorsal position than the main trunk, and, further distally, rejoins the main trunk (or the dorsal trunk described below). This bundle sends off fibres which are lost in the surrounding connective tissue. The main trunk of the ophthalmicus gives off such fibres both behind and in front of the eye in all the specimens studied. At the rostral boundary of the nasal capsule, the dorsal trunk of r. palatinus loses contact with the ophthalmicus, and it is possible that some ophthalmic fibres accompany the palatinus nerve. Rostral to this point n. ophthalmicus is separated from "the palatine bar" by m. trabeculo-subnasalis profundus. The nerve divides into a dorsal and a ventral trunk, both of which continue chiefly rostrad.

The ventral trunk (fig. 9, *n.oph.III*) runs in a space surrounded by the nasal duct, m. trabeculo-subnasalis superficialis and m. trabeculo-subnasalis profundus. Further rostrally, the nerve lies between the two muscles. Still further rostrally, it runs inside m. trabeculo-subnasalis superficialis and appears

again on the lateral surface of the muscle in the region where the muscle has its origin on the subnasal cartilage. In the continuation the nerve runs along the dorsal side of the surface of contact between m. subnasali-basalis and m. subnasali-tentacularis, crosses further distally the dorsal surface of m. subnasali-tentacularis and comes into contact with m. transversus oris sensu stricto (COLE, 1908). Here the ventral trunk of the ophthalmicus divides into two branches. One branch (*n.oph.IIIa*) bends off ventrad between m. subnasali-tentacularis and m. transversus oris sensu stricto, running ventral to the transverse root piece of the tentacle cartilage II. The branch pierces the commissure of m. transversus oris, which lies dorsal to the mouth opening (COLE's ventral commissure, 1908), and spreads out in the skin rostral to the mouth opening. According to COLE m. transversus oris sensu stricto does not contribute any muscle fibres to the ventral commissure. It is difficult to delimit the two muscles but if there is a boundary, the branches of the ophthalmicus pass between the ventral commissure and m. transversus oris sensu stricto. The other branch from the ventral trunk of the ophthalmicus (*r.tent.II*) continues rostrad up to the tentacle cartilages II and forms a sheath around the skeletal element. (In P. FÜRBRINGER's terminology it is tentacle 1).

The proximal part of the dorsal trunk of the ophthalmicus (*n.oph.II*) lies between the nasal duct and m. trabeculo-subnasalis superficialis, ventral to m. nasalis. Further rostrally, m. trabeculo-subnasalis superficialis is replaced by m. nasalis on the lateral side of the nerve. A branch is here given off dorsolaterad through m. nasalis to the skin. This is repeated further rostrally in at least two places. FÜRBRINGER probably interpreted these branches as motor branches to m. nasalis, since he reports that a number of muscles, among them m. nasalis, are innervated by n. ophthalmicus. POLLARD (1894) makes the same statement. In approximately the transverse plane through the rostral boundary of the subnasal cartilage, the dorsal trunk of the ophthalmicus splits up into a number of branches which run some to the skin on the tip of the snout, dorsal to the orifice of the nasal duct, and some to a fold of skin between tentacles I and II. No branches of the ophthalmicus running to tentacle I could be observed.

Summary. N. ophthalmicus runs dorsal to n. opticus and gives off, rostral to this point, a branch running to the skin in front of the eye. Further distally, ophthalmicus divides into two trunks. The ventral trunk runs to tentacle II and to the skin rostral to the mouth opening. The dorsal one gives off, during its course, some branches to the skin outside the nasal duct. The rest of the dorsal trunk innervates the tip of the snout.

Discussion. The supposed existence of motor fibres in the ophthalmicus in the Myxinids prevented during the 19th century a comparison of the nerve with the ophthalmicus in the Gnathostomes. ALLIS (1903, Bdellostoma) was the first to state that the ophthalmicus in a Myxinid is purely

sensory. AYERS (1921, Bdellostoma) returned to the view taken by the older writers that the nerve contains a motor component. This is contradicted, however, by investigations carried out on the central nervous system. Studies of the medulla in Myxine show that the ophthalmicus contains a general cutaneous component (HOLMGREN, 1919, JANSEN, 1930). A curious fibre bundle, coming from cell bodies in the utricular ganglion and passing to n. ophthalmicus, is described by HOLMGREN. He considered it to consist of acustico-lateralis fibres. JANSEN confirmed the existence of the fibre bundle, but was of the opinion that it contained general cutaneous fibres. HEIER (1948, p. 189) possibly alludes to this fibre bundle when he makes a comparison with the acoustic fibres in Petromyzon, which in the nucleus octomotorius medius, are connected to neurons whose fibres leave the brain with the motor trigeminus. HEIER considers it possible that the fibres joining the trigeminal nerve are destined for nervus abducens in Petromyzon. However, the utricular-trigeminal fibres in Myxine run out into n. ophthalmicus and a n. abducens is absent in this fish. HEIER's comparison does not appear so well established. According to AYERS—WORTHINGTON's studies of the nuclear region and the pehipheral end region of the ophthalmicus in Bdellostoma (1908 a and b, 1911), the nerve contains a general cutaneous component, but these two authors state that in addition, a lateralis and a fasciculus communis component is distributed to the anterior and posterior sensory trunks of the trigeminus. The "posterior trunk" in their description is the nerve called here n. buccalis. The anterior trunk is the trigeminus proper. It is not clear from AYERS—WORTHINGTON's description, to which branches of the trigeminus (n. ophthalmicus, r. externus?) the lateralis and communis fibres run. If Bdellostoma has a lateralis component in the ophthalmicus which is possibly lacking in Myxine this condition may be connected with the fact that lateralis organs have been observed only in Bdellostoma. On the other hand, a possible difference between the two genera regarding the occurence of communis fibres seems to be more difficult to explain (see p. 421).

Certain details in the peripheral course of the ophthalmicus must be considered more closely. ALLIS (1903) discovered that "r. nasalis ophthalmicus" in Bdellostoma was actually a branch of r. palatinus (see p. 337). This does not however dismiss the conception of the ophthalmicus innervation of the nasal duct and the nasal capsule in Bdellostoma. As a matter of fact MÜLLER (1839), ALLIS (1903) and WORTHINGTON (1906) mention that the dorsal trunk of the ophthalmicus innervates the nasal duct. No such observation has been made on Myxine, but it should be pointed out here that some ophthalmic fibres may possibly join the dorsal trunk of r. palatinus where the ophthalmicus and the palatinus trunk separate.

ALLIS (p. 267) states that the ventral trunk of the ophthalmicus in Bdellostoma contains both fibres destined for tentacle II and fibres to the skin

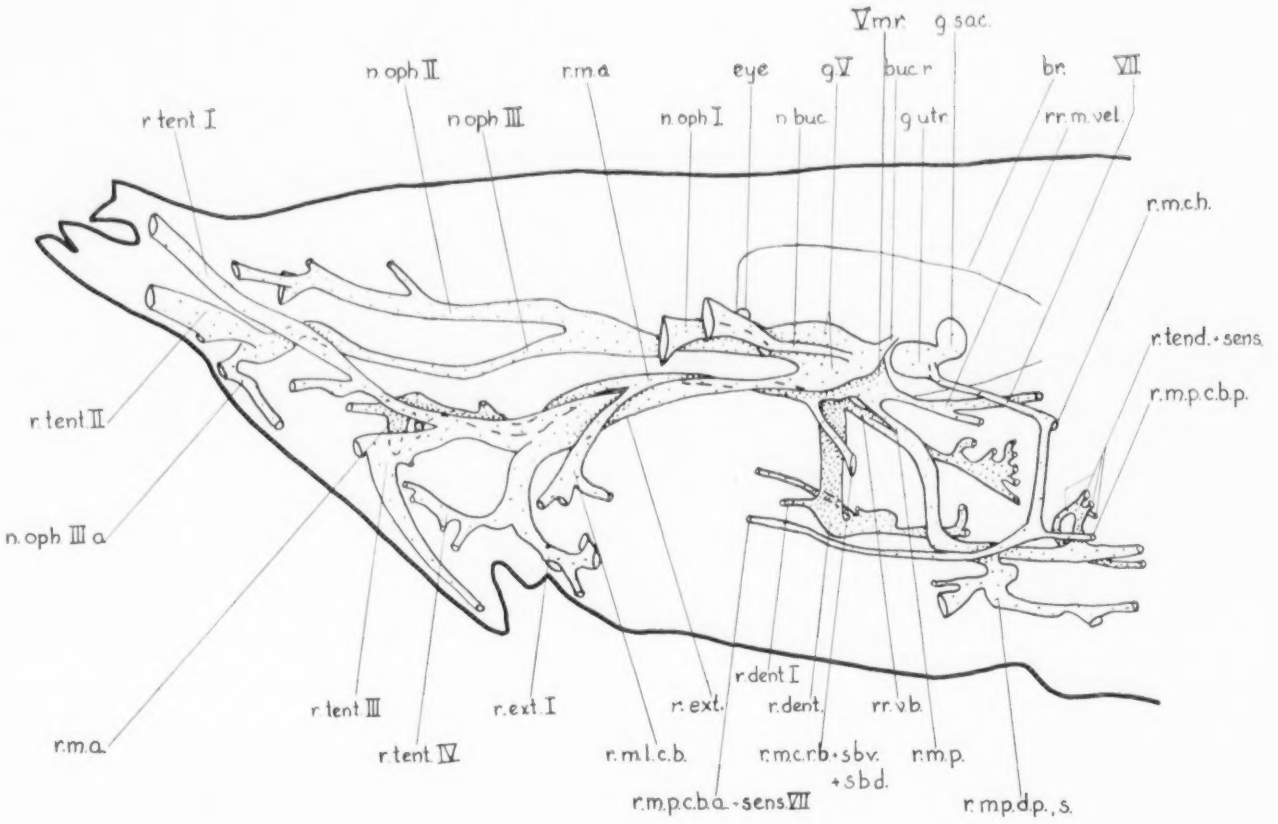

Fig. 9.

Fig. 9. Myxine, adult. Reconstruction of n. trigeminus, n. buccalis, n. facialis and the acoustic ganglia. Lateral view. 11 ×.

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surrounding the tentacle. Most of the latter fibres run in an "important branch", dorsal to "the transverse labial cartilage"—i.e. the base of the tentacle cartilage II—and then pierce the ventral commissure of m. transversus oris. It is clear from the description on page 327 of the present paper that the relationship between the nerve and the tentacle cartilage is the same in the Bdellostoma embryo. In Myxine, however, the most closely corresponding branch of the ophthalmicus runs ventral to the skeletal bar.

AYERS (1921) mentions an anastomosis between the ophthalmicus and the opticus in Bdellostoma. The present author has not been able to verify the existense of such an anastomosis in Myxine.

Apart from these differences, the agreement between the peripheral courses and the end regions of the ophthalmicus in Myxine and Bdellostoma appears to be good.

B. The V_2-Complex.

The V_2-ganglion lies ventral and caudal to the ophthalmic ganglion. From it emerge the following nerves: two nerves running chiefly rostrad, one running ventro-caudad (p. 342) and, finally, a small bundle of fibres mentioned on page 345. The nerves running rostrad are r. externus, which passes through the subocular fenestra, and r. palatinus.

a. *Sensory Branches running Rostrad.*

R. palatinus (fig. 10) emerges from a portion of the ganglion projecting mediad, ventral to the brain capsule and dorsal to the anterior connection between the trabecle and the dorsal longitudinal bar (fig. 14, *g.V pal.*). This nerve was not observed by P. FÜRBRINGER (1875). It consists of three trunks, two of which run chiefly rostrad and the third chiefly caudad.

One of the rostral trunks (fig. 10, *r.pal.I*) runs in a more dorsal position than the other palatinus branches and is destined for the nasal capsule and the nasal duct. It passes between the dorsal longitudinal bar and the brain, ventral to n. opticus and well separated from n. ophthalmicus. At the caudal part of the nasal capsule it draws closer to n. ophthalmicus. Along the nasal capsule, the trunk of the palatinus runs close up against the medial side of the ophthalmicus and in many specimens it is difficult to delimit the nerves. In a few specimens it can be done, however, even if it is impossible to check whether there is an exchange of single fibres. It seems possible—judging from the sections—that a small bundle of ophthalmicus fibres accompany the palatinus trunk in its subsequent course. At the anterior part of the nasal capsule, the palatinus trunk separates from the ophthalmicus and bends off dorso-rostrad (*r.pal.I, oph.?*). At the same time it gives off a small branch caudad. This branch can be traced into the rostral part of the nasal capsule where it is lost. After giving

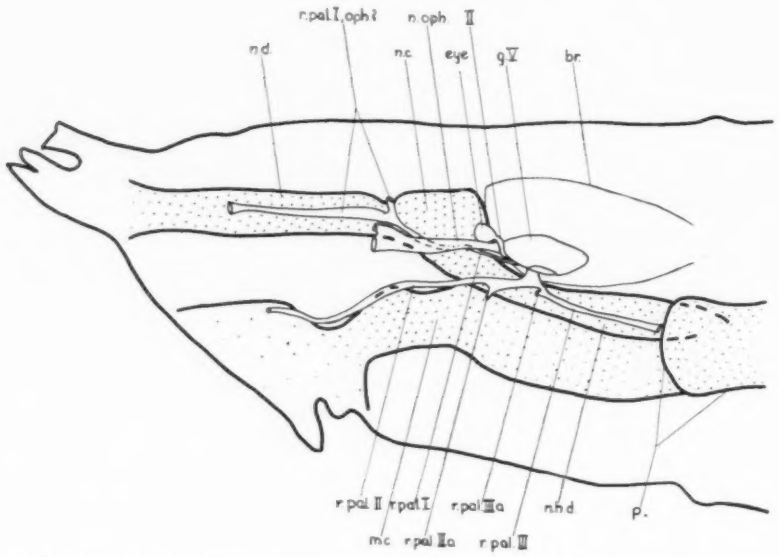

Fig. 10. Myxine, adult. Reconstruction of r. palatinus. The rest of the V_2-nerves and part of n. ophthalmicus are omitted. Lateral view. 7 ×.

off this branch, the palatinus trunk runs rostrad again, along the side of the nasal duct, lateral to the skeletal rings. Branches are given off between the skeletal rings running both to the dorsal and to the ventral regions of the mucous membrane of the duct. The palatinus trunk can be traced quite definitely as far as the third skeletal ring from the front.

The other rostral and the caudal palatinus trunks leave the ganglion together (fig. 11) and the joint nerve passes ventrad through an incomplete skeletal fenestra. The sides of the fenestra are formed by the following structures: the dorsal longitudinal bar laterally, the anterior connection between this bar and the trabecle caudo-laterally, and finally the trabecle caudo-medially, medially and rostro-medially. In the adult Myxinids the trabecles run inwards towards the hypophysial cartilage and then bend off rostro-laterad out towards the nasal capsule (cf. HOLMGREN, 1946). In this incomplete fenestra the joint nerve divides into a rostral and a caudal trunk.

The rostral trunk (figs. 10, 11, *r.pal.II*) runs ventral to the part of the trabecle lying between the hypophysial cartilage and the nasal capsule. Further distally, the nerve trunk passes medial to m. craniovelaris and the medial head of m. trabeculo-coronarius. In the region below the eye, it gives off a branch caudad along the medio-dorsal fold in the wall of the buccal cavity, innervating the mucous membrane there (fig. 10, *r.pal.IIa*). This branch can be traced to at least the region below the trigeminal ganglion. The rest of the palatinus trunk continues rostrad, runs ventral to "the palatine bar" and lies

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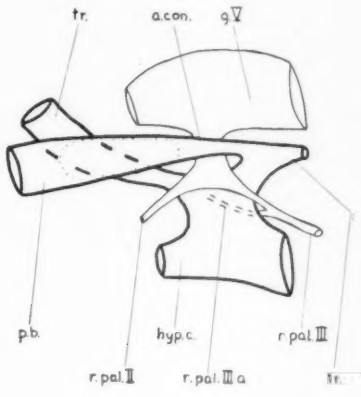

Fig. 11. Myxine, adult. Reconstruction of the ventral branches of r. palatinus and adjacent skeletal bars. The dorsal longitudinal bar is cut off along the surface indicated by the dotted line. Lateral view. 22 ×.

in its subsequent course in the wall of the buccal cavity, innervating this. Some fibres are sent off to the dorsal "palatine tooth", whereas the trunk passes on the lateral side of the tooth. The nerve trunk can be traced to the dorsal boundary of the mouth opening.

After passing through the incomplete fenestra, the caudal palatinus trunk (figs. 10, 11, *r.pal.III*) runs ventral to the part of the trabecle lying between the hypophysial cartilage and the "anterior connection" of the trabecle. Here it sends off a branch (*r.pal.IIIa*) which passes caudal—medial to the said part of the trabecle and which can be traced rostrad in the naso-hypophysial duct to a point underneath the rostral part of the nasal capsule. The fibres of the branch are lost in the mucous membrane of the duct. The caudal trunk of the palatinus thus curves round the trabecle. The last mentioned branch completes the curve into a full spiral turn. The caudal palatinus trunk continues caudad along the naso-hypophysial duct, separated from it by the hypophysial-velar sinus (COLE, 1926), and in so doing passes medial to m. craniovelaris. At the caudal part of the hypophysial cartilage, the nerve runs ventral to the naso-hypophysial duct and is lost in the walls of this duct.

R. externus. This nerve was called by P. FÜRBRINGER (1875) "r. externus anterior superficialis" of n. maxillaris. FÜRBRINGER says, however, that m. levator cartilaginis basalis is innervated by the nerve. As will be shown later (p. 348), this muscle is innervated by a more medial trigeminal trunk.

After passing the subocular fenestra, r. externus (fig. 9, *r.ext.*) continues rostrad running dorsal to m. flexor trabeculae and ventral to the anterior connection between the trabecle and the dorsal longitudinal bar. R. externus lies lateral to r. muscularis anterior. A little further rostrally, r. externus is found between m. flexor trabeculae and the lateral head of m. trabeculo-coronarius.

In one of the specimens studied a branch is given off here in the region

below the eye. The branch passes between m. cranio-basalis and the lateral head of m. trabeculo-coronarius. The branch bends laterad over the dorsal edge of m. cranio-basalis, runs ventrad along the lateral side of the muscle and reaches the surface of contact between m. tentacularis posterior and the spinal musculature. Here the branch turns laterad and runs out to the skin. This branch was not found in the other specimens—at least not in the position described.

We shall now return to the description of the normal course of r. externus. At the place where m. flexor trabeculae passes into its tendon, the nerve runs in the space between the wall of the buccal cavity, m. trabeculo-coronarius and m. cranio-basalis. Further rostrally the nerve also gets in contact with the surface of m. trabeculo-subnasalis superficialis (dorsally) and, in certain specimens, with the surface of m. protractor cartilaginis basalis anterior also (laterally). In this region the nerve and r. m. levator cartilaginis basalis intersect (p. 348). R. externus breaks up into two trunks which run further rostrad and side by side.

Further rostrally, on the medial side of the now divided nerve, m. trabeculo-coronarius is inserted and r. externus runs along r. muscularis anterior. On the ventro-medial side of r. externus lies the labial cartilage. R. externus now runs on the medial side of m. levator cartilaginis basalis. Somewhat further rostrally, m. subnasali-basalis lies between the nerve and the labial cartilage. At the same time the two trunks of r. externus separate.

One trunk bends off ventrad immediately caudal to the lateral head of m. subnasali-basalis and runs between m. levator cartilaginis basalis (laterally) and the medial head of m. subnasali-basalis and m. basali-tentaculo-labialis (both medially). The trunk now divides into a rostral and a caudal branch. The caudal branch (*r.ext.I*) runs subcutaneously outside m. basali-tentaculo-labialis to the skin on the lateral and ventral sides of the mouth opening. One bundle from the branch (not pictured) can be traced caudad in the medio-ventral wall of the buccal cavity towards the front edge of the dental plate. The rostral branch of the nerve trunk (*r.tent.IV*) runs subcutaneously outside m. basali-tentaculo-labialis and innervates the skin in the vicinity of tentacle IV and the tentacle itself.

The dorsal trunk of r. externus runs between the cornual cartilage (dorsally) and m. subnasali-basalis (ventro-medially). The nerve trunk runs lateral to r. muscularis anterior, close to this nerve. Rostral to m. levator cartilaginis basalis, the nerve trunk splits up into two branches: r. tentaculi III and r. tentaculi I. The former (*r.tent.III*) runs ventrad between m. tentacularis posterior and the part of m. basali-tentaculo-labialis situated along the caudal side of the tentacle cartilage III. R. tentaculi III gives off branches to the skin in the vicinity of the tentacle and finally forms a sheath of nerve fibres between the skeletal element and the skin on the tentacle. R. tentaculi I (*r.tent.I*) maintains

a rostral course and a position ventral to the cornual cartilage. M. tentacularis posterior lies on the lateral side of the nerve. On the medial side of the nerve lie the part of m. basali-tentaculo-labialis mentioned above and the tentacle cartilage III. Further rostrally, the nerve loses contact with the cornual cartilage, runs medial and ventral to m. tentacularis posterior and sends off bundles of fibres to the skin of the rostro-lateral region of the snout. Some bundles pass through the muscle and some through the fascia ventral to the muscle. At the rostral boundary of the muscle, the tentacle cartilage I lies on the medial side of the nerve and the nerve fibres group themselves round this cartilage into a sheath between the skeletal element and the skin on tentacle I.

According to P. FÜRBRINGER (1875), "r. externus anterior superficialis" of the "maxillaris" innervates tentacles "2" and "3" (i.e. tentacles I and III in the present nomenclature). On the other hand, the region round tentacle IV is said to receive sensory nerve fibres from another nerve, in the present paper called r. muscularis anterior. This is not in accordance with the observations on the present material, as all the sensory fibres in tentacle IV and in its surroundings come from r. externus.

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S u m m a r y. R. palatinus issues in three trunks from a portion of the ganglion projecting mediad. One trunk runs dorsal to the trabecle and "the palatine bar", but ventral to n. opticus, and joins n. ophthalmicus on the medial side of the latter. Further distally, this palatinus trunk separates again from the ophthalmicus (whereby it is possible that some ophthalmicus fibres accompany the palatinus trunk) and innervates the nasal duct and the rostral part of the nasal capsule. The other two palatinus trunks issue as a common nerve, running ventrad through a skeletal fenestra bounded by the trabecle, the dorsal longitudinal bar and the anterior connection between these skeletal bars. Here the two trunks divide and the rostral one innervates the mediodorsal wall of the buccal cavity between the region below the trigeminal ganglion and the mouth opening, whereas the caudal trunk innervates the nasohypophysial duct. These last two palatinus trunks lie medial to r. muscularis anterior. R. externus passes through the subocular fenestra and runs rostrad, lateral to r. muscularis anterior. The nerve and its branches lie lateral to the labial cartilage at the points where nerve and cartilage cross. The ventral branches supply tentacle IV, the skin laterally and ventrally in the mouth opening, and the most anterior part of the ventral wall of the buccal cavity. R. externus' dorsal branches lie ventral to the cornual cartilage and spread out to tentacles I and III and the adjacent skin round the mouth opening.

L i t e r a t u r e o n B d e l l o s t o m a. From the various descriptions of the trigeminus in Bdellostoma it is possible to arrive at an account of a r. palatinus which could also be applied to r. palatinus in Myxine. In each individual paper on Bdellostoma there are, however, certain important divergencies from the present observations on Myxine. MÜLLER, as early as 1839, showed

how the course of the nerve differed from those of the other V_2-branches. He says that branch No. "9" passes between "die mittlere Gaumenplatte" and "die seitliche Gaumenleiste". ALLIS (1903, Bdellostoma) was the first and only writer to give an essentially correct description of r. palatinus in the Myxinids. His description differs from the present observations on Myxine only in so far as he says that the dorsal trunk cannot be traced further than "slightly beyond the nasal capsule". The most recent description of r. palatinus in Bdellostoma is AYERS's (1921). He states that the dorsal trunk of the palatinus ("nasalis") sends off fibres to the opticus and innervates m. nasalis. It has not been possible to confirm any of these statements on the present material.

ALLIS (l.c.) was also the first to give a correct description of r. externus in as much as he points out that tentacle IV and its surroundings are innervated by a branch of r. externus, whereas m. levator cartilaginis basalis is innervated by another trunk of the trigeminus. AYERS (1931, p. 357) describes a branch of the "maxillaris" which is probably identical to the branch of r. externus running caudad in the ventral wall of the buccal cavity in Myxine and innervating the mucous membrane rostral to the dental plate. According to AYERS, however, this branch also innervates the most anterior part of the dental plate.

b. *Sensory Branches running Ventro-Caudad.*

These issue from the ventral side of the V_2-ganglion as a combined nerve pointing ventrad. Its point of exit lies caudal to that of r. externus. The nerve runs down through the subocular fenestra, lateral to m. craniovelaris and medial to rr. musculares. Dorsal to m. flexor trabeculae, the nerve divides into a large branch, r. dentalis (fig. 9, *r.dent.*) and a number of smaller branches, rr. velobuccales (fig. 9, *rr.v.b.*).

Rr. velobuccales are three or four in number (P. FÜRBRINGER's "rr. palatini" of "r. maxillaris externus medius", 1875). They run ventrad to ventro-caudad between m. flexor trabeculae and m. craniovelaris to the dorsal wall of the buccal cavity where the most anterior branch (fig. 12, *rr.v.b.I*) divides into a caudal and a rostral bundle. In some specimens a second branch exists, running in the same course as the most anterior branch just described. The two (four) bundles can be traced a short distance in the latero-dorsal wall of the buccal cavity: one bundle running rostrad could be quite definitely traced as far rostrad as the region below the eye. The two caudal branches of rr. velobuccales run together for a certain distance as one trunk and then separate. One branch (fig. 12, *rr.v.b.II*, cf. fig. 9) joins up with r. muscularis posterior and another runs caudad in a band of connective tissue lying dorso-lateral to the buccal cavity.

From this last branch, nerve bundles are repeatedly given off mediad to

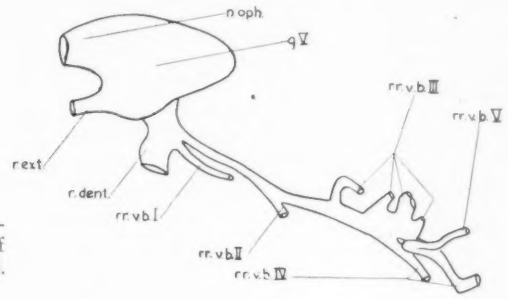

Fig. 12. Myxine, adult. Reconstruction of rr. velobuccales. The rest of the trigeminal nerves are omitted. Lateral view. 16 ×.

the mucous membrane of the buccal cavity (but not to its ventral and dorso-medial parts). Immediately rostral to the caudal orifice of the naso-hypophysial duct, the branch splits up into a large number of fibre bundles. Of these, the dorsal bundles (fig. 12, *rr.v.b.III*) supply the mucous membrane on the rostral side of the orifice richly with nerve fibres. The ventral bundles (*rr.v.b.IV*) can be traced in the lateral and ventral walls of the buccal cavity a certain distance caudal to the said orifice. One bundle of fibres, finally describes a loop, running first rostrad, then latero-dorsad and finally caudad (*rr.v.b.V*). The bundle runs in the lateral part of the velum, lateral to the skeletal element and close against the mucous membrane. In this position the bundle can be traced caudad at least as far as the point where the velar bar divides. No trigeminal innervation of the dorsal wall of the digestive tract between the velar ridges could be observed. The loop described above is probably conditioned by the mobility of the velum. According to GUSTAFSON (1936) it is the velum that pumps forth the respiratory water. COLE (1926) thought that the mobility of the velum is linked up with the circulation of the blood since the cardinal heart is rhythmically compressed by the movements of the velum. In order to avoid tension, the nerve runs in a loop so that it can stretch when necessary.

The sensory branch which joins up with r. muscularis posterior cannot in its subsequent course be delimited with any degree of certainty from the motor nerve. The following sensory branches are given off from the mixed trunk. When the nerve trunk is near the contact between the medium paired basal plates and the unpaired caudal basal plate, a nerve is given off which describes a loop in the sagittal plane. From the ascending, caudal half of the loop a number of small bundles of fibres are given off (see fig. 15) to the ventral wall of the buccal cavity. Some of the bundles could be traced with certainty to a position caudal to the region below the posterior orifice of the naso-hypophysial duct. After these bundles have been given off, the nerve loop encounters the corresponding nerve from the other half of the body in the medial line, and the joint, downward, i.e. cranial, part of the loop gives off a

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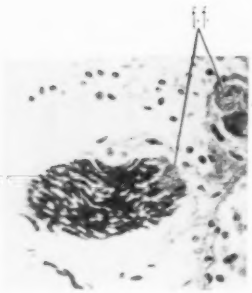

Fig. 13. Myxine, adult. The mixed nerve, formed by r. muscularis posterior and a branch of rr. velobuccales. Transverse section. 190 ×.

sensory branch which runs rostrad in the connective tissue between the tendon of m. clavatus and the wall of the buccal cavity, caudal to the dental plate, and innervates the mucous membrane of the buccal cavity there. The nerve loop itself runs caudad into the tendon of m. clavatus (fig. 15, *r.tend.*). Inside the tendon, the nerve again divides into a branch to each half of the body. Some of the nerve fibres are lost in the tendon, but the rest continue caudad and are lost in the boundary region between the tendon and the muscle and to some extent in the muscle. M. clavatus is supplied with motor fibres from elsewhere (p. 350), so it is tempting to guess that the nerve fibres described here transmit impulses from end organs, registering the tension. The present author did not observe any sensory end organs in the tendon or in the muscle. (Such end organs have been described by ALLEN, 1917, in m. cordis caudalis in Bdellostoma.) The question as to the character of the nerve fibres must nevertheless be left open for the time being, because these fibres are of the same calibre as the motor fibres in rr. musculares. On the other hand, the fibres in the branch of rr. velobuccales which join proximally with r. muscularis posterior and the fibres which leave the mixed trunk distally and are lost in the mucous membrane of the buccal cavity are clearly smaller in calibre (fig. 13). This is, of course, a strong indicium of continuity between the branch from rr. velobuccales and the fibres which run out distally into the mucous membrane.

P. FÜRBRINGER (1875) calls the entire nerve loop just described "r. pro lingua" of "r. maxillaris internus". As the end region, however, he gives only the posterior regions of the mucous membrane of "die Zungenplatte".

The significance of the looped shape of the nerve appears to be to prevent tension of the nerve, which might otherwise be caused by the movement of the dental plate.

R. d e n t a l i s is called by P. FÜRBRINGER "r. maxillaris externus posterior" and said to contain motor fibres to m. cranio-basalis. There are, however, no motor fibres in r. dentalis. After the nerve (fig. 9, *r.dent.*) leaves the common sensory trunk (p. 342), it bends ventro-laterad and cuts through m. flexor trabeculae or passes lateral to this muscle. Further distally, the nerve runs

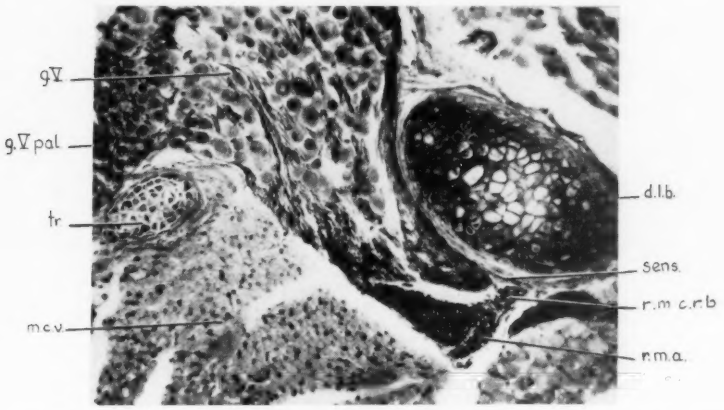

Fig. 14. Myxine, adult. The origin of a mixed nerve formed by branches from r. muscularis anterior and from the lateral part of the V_2-ganglion (sens.). Transverse section. 120 ×.

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first ventrad and then mediad round the buccal cavity, medial to m. cranio-basalis. The nerve cuts through the most anterior part of m. retractor mucosae oris in most specimens. When it has reached a position ventral to the dental plate and dorsal to the basal plates, it sends off a branch rostrad. (Only the proximal part of the branch is shown in fig. 9, *r.dent.I.*) The branch runs in the ligament forming the rostral continuation of m. retractor mucosae oris. The branch lies thus between the dental plate and m. cranio-basalis. Further rostrally it runs between the lateral frontal basal plate and the wall of the buccal cavity. This branch can be traced to the anterior border of the basal plates and ends probably in the skin in the ventro-lateral part of the mouth opening. Here is, thus, an area innervated by r. dentalis wedged in between an area innervated by the ventral trunk of r. externus and one innervated by r. palatinus. After r. dentalis has given off the branch just described, it takes up a medial course and splits into rostral and caudal branches which are lost in the dental plate.

c. *Sensory Branch to the Vicinity of the Basal Plates.*

From the V_2-ganglion is given off, finally, a bundle of fibres (fig. 14, *sens.*) which joins r.m. cranio-basalis. This sensory bundle of fibres could certainly have been described together with the "Sensory Branches running Ventro-Caudad", but the bundle issues from the lateral part of the ganglion and passes lateral to rr. musculares, whereas rr. velo-buccales and r. dentalis run medial to the motor trunk. This difference in position will play an important part in later discussions (p. 437), and is the reason why this bundle of fibres is being dealt with under a special heading. The fibres in the bundle emerging

from the ganglion are finer in calibre than those of the motor r.m. cranio-basalis. From the mixed nerve (figs. 9, 15, *r.m.c.r.b.+s.b.v.+s.b.d.*, fig. 46, *r.m.cr.b.+sens.*) are given off a number of branches destined for m. cranio-basalis and in addition fibres which run further ventrad, medial to m. cranio-basalis, and are lost in the immediate vicinity of the medium paired basal plates and the unpaired caudal basal plates. Whereas, as far as the present author could discover, all the fibres innervating m. cranio-basalis are rather thick in calibre, the fibres which are lost near the basal plates are fine. This is a strong indicium that the latter fibres are identical with the fine fibres originating in the ganglion. After separating themselves from the motor branches, most of the fine fibres are collected proximally into one bundle. This runs ventro-caudad passing lateral to a blood vessel. The blood vessel (fig. 46) is a branch of the lingual artery (HOLMGREN, 1946) and divides in its turn into an artery to the dorso-lateral wall of the buccal cavity and one which passes through a ligament belonging to m. retractor mucosae oris. The last mentioned vessel terminates in the dental plate. All the data indicate that the branch of the lingual artery is identical with a. palatina according to GRODZIŃSKI's (1927) or the posterior lingual artery according to COLE's terminology (1926). The nerve bundle gives off single fibres, but most of it runs in one nerve bundle, lateral and ventral to the lingual artery (HOLMGREN). The bundle divides into two, and one branch is lost ventral to the medium paired basal plates (fig. 46, *s.b.v.*). The other one runs dorsad between the artery and the skeletal element (*s.b.d.*, cf. also fig 21) and bends caudad, running along the lateral wall of the unpaired caudal basal plate. This nerve bundle passes ventral to r. muscularis posterior and is lost on the inside of the wall of the caudal basal plate. The fine calibre nerve fibres described above may be either proprioceptive or visceral afferent (coming from blood vessels) or autonomic, i.e. motor.

The summaries of the courses of the Sensory Branches running Ventro-Caudad and of the nerve just described and the discussion of the literature on the corresponding nerves in Bdellostoma will be postponed until page 351.

d. *Rr. Musculares Trigemini.*

The main motor trunk passes through the subocular fenestra. Ventro-caudal to the V_2-ganglion, the trunk divides into r. muscularis anterior, r. muscularis posterior and rr. musculares velares (fig. 15). R. muscularis anterior (*r.m.a.*) runs rostrad between m. craniovelaris and the dorsal longitudinal bar. The nerve passes lateral to the ventro-caudally directed sensory branches of the trigeminus, and gives off r.m. cranio-basalis laterad. This branch runs between m. flexor trabeculae and the dorsal longitudinal bar and joins a sensory bundle from the lateral part of the ganglion (p. 345). The mixed

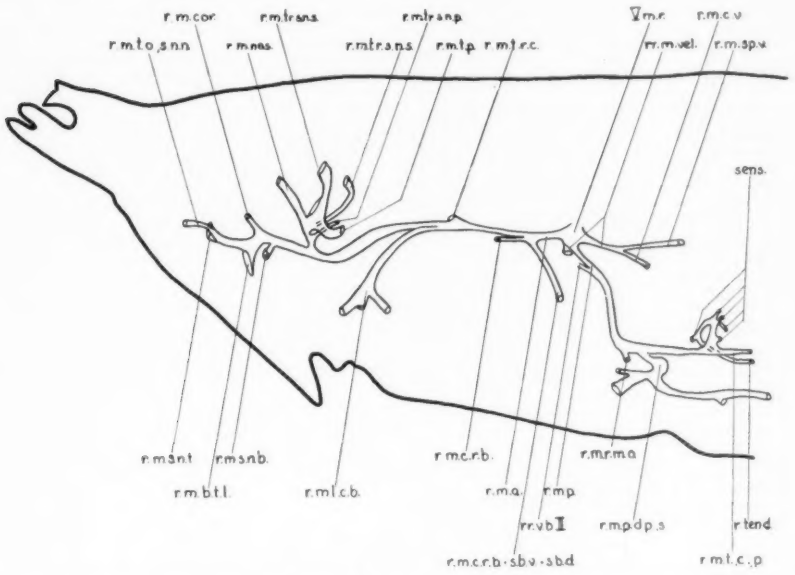

Fig. 15. Myxine, adult. Reconstruction of the motor trigeminal nerves. Lateral view. 7 ×.

nerve runs rostrad to the region below the rostral boundary of the subocular fenestra, where it bends off laterad and runs between m. flexor trabeculae (ventrally) and the dorsal longitudinal bar and the lateral head of m. trabeculo-coronarius (dorsally). The nerve divides into two branches. One runs rostrad on the medial side of m. cranio-basalis and innervates the dorso-rostral part of this muscle. The other branch runs ventro-caudad between m. flexor trabeculae and m. cranio-basalis, passing lateral to r. dentalis, and continues ventrad close against the wall of the buccal cavity. The nerve branch gives off fibres innervating m. cranio-basalis and the fine calibre fibres described on page 346.

Distal to the point where r. muscularis anterior gives off r.m. cranio-basalis, r. externus approaches r. muscularis anterior. The sensory nerve runs along the lateral side of the motor nerve thus separating the motor nerve from the dorsal longitudinal bar. The motor nerve runs close beside m. flexor trabeculae and m. craniovelaris and passes ventral to the anterior connection between the trabecle and the dorsal longitudinal bar. Further rostrally the medial head of m. trabeculo-coronarius lies on the medial side of r. muscularis anterior. Still more rostrally m. flexor trabeculae passes into its tendon and r. muscularis anterior lies between the medial and the lateral head of m. trabeculo-coronarius. In the same transverse region, r. externus runs out into a more lateral position, i.e. the two nerves lose contact with each other. R. muscularis anterior gives off both a number of scattered bundles of fibres which innervate the two heads of m. trabeculo-coronarius (*r.m.tr.c.*), and

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r.m. levator cartilaginis basalis (*r.m.l.c.b.*). R.m. levator cartilaginis basalis runs laterad towards r. externus and clings closely to r. externus first on the medial, then on the dorsal and finally on the lateral side of the sensory nerve (normally). The course of the motor branch is, however, different in different specimens. In one specimen the branch runs instead along the medial and ventral sides of r. externus. In the region lateral to the most anterior part of "the palatine bar", r.m. levator cartilaginis basalis changes (in all specimens) its direction to ventro-rostral and loses contact with r. externus. The motor branch runs along the medial sides of m. protractor cartilaginis basalis anterior and m. levator cartilaginis basalis. Close to the latter muscle, the nerve divides into rostral and caudal bundles of fibres which innervate m. levator cartilaginis basalis.

After r. muscularis anterior has given off r.m. levator cartilaginis basalis it is surrounded in its subsequent and still rostral course by m. trabeculo-coronarius, except on the medial side where "the palatine bar" is situated. As the muscle, further rostrally, is inserted, the nerve again runs alongside r. externus, passing between the labial cartilage and the basal part of the cornual cartilage. Further rostrally, these two skeletal elements change their position so that the cornual cartilage occupies a more lateral and the labial cartilage a more medial position. R. muscularis anterior divides into two trunks.

One trunk bends off dorsad, medial to the cornual cartilage, and pierces m. trabeculo-subnasalis profundus near to its insertion on the cornual cartilage. From this trunk a bundle of nerve fibres is sent off into the muscle (*r.m.tr.s.n.p.*). These fibres run partly inside the muscle and partly on its dorsal surface, innervating the muscle. The remainder of the trunk ramifies into four or more branches. The ramification point lies in a space surrounded by m. trabeculo-subnasalis sup. and prof. and m. tentacularis posterior. One branch follows a certain distance along the medial side of m. tentacularis posterior and ramifies into the muscle (*r.m.t.p.*). Another runs along the ventral and medial sides of m. trabeculo-subnasalis sup., passes latero-dorsal to the ventral trunk of n. ophthalmicus and finally ramifies in m. trabeculo-subnasalis sup. (the posterior *r.m.tr.s.n.s.*). A third branch runs chiefly dorsad along the lateral surface of m. trabeculo-subnasalis sup. and ramifies into the muscle (the anterior *r.m.tr.s.n.s.*). The course of the fourth branch is similar, but it continues up to m. nasalis which it innervates (*r.m.nas.*).

The other trunk of r. muscularis anterior runs lateral to the labial cartilage and dorsal to m. subnasali-basalis. Further distally, the trunk moves via the dorsal side to the medial side of the cartilage, still dorsal to m. subnasali-basalis. Still further distally (rostrally), the muscle lies both ventral and medial to the nerve. Here, the nerve sends off first some branches which innervate m. subnasali-basalis (*r.m.s.n.b.*) and then a branch running ventral and lateral to the labial cartilage up to m. coronarius (*r.m.cor.*). Rostral to the

branches just mentioned, the nerve trunk sends off yet another branch (*r.m.b.t.l.*) running ventrad between m. subnasali-basalis and the part of m. basali-tentaculo-labialis which lies caudal to the tentacle cartilage III. The branch innervates the said part of m. basali-tentaculo-labialis and in addition the main part of the muscle further ventrally. The remaining nerve trunk continues rostrad, running along the lateral side of m. subnasali-basalis and, further distally, lateral to m. subnasali-tentacularis and medial to m. transversus oris sensu stricto (COLE, 1908). The nerve trunk sends off branches which innervate m. subnasali-tentacularis and m. transversus oris sensu stricto (*r.m.s.n.t.*) The most distal branches of the nerve trunk innervate m. subnasali-nasalis and the commissures of m. transversus oris (*r.m.t.o., s.n.n.*). These end branches run mediad, some ventral to all the branches of the ophthalmicus (apart from the retrogressive ophthalmic branches running in the skin in front of the mouth opening) and some between the ventral branches of the ventral trunk of the ophthalmicus.

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P. FÜRBRINGER'S view (1875) that n. ophthalmicus innervates certain muscles, has led him to allot too few muscles to "r. externus anterior profundus", i.e. r. muscularis anterior.

R. muscularis posterior. After separating from r. muscularis anterior, the nerve (fig. 15, *r.m.p.*) has a ventro-caudal course and runs between m. craniovelaris and the dorsal longitudinal bar. Further caudally, where the extra-mandibular has separated from the dorsal longitudinal bar, the nerve runs medial to the extra-mandibular and dorsal to the caudal part of m. flexor trabeculae. Here, the nerve gives off a branch which innervates m. flexor trabeculae. Then the nerve unites with the sensory branch from rr. velobuccales described on page 342 (fig. 15, *rr.v.b.II*). The mixed nerve which results was called "r. maxillaris internus" by P. FÜRBRINGER. His description applies on the whole to the present material. The nerve has an almost straight ventral course between m. cranio-basalis and the wall of the buccal cavity. (R. muscularis posterior can be divided in its course described hitherto into several trunks which join up here again.) The mixed nerve trunk bends off caudad, runs between m. cranio-basalis and m. retractor mucosae oris, and gives off bundles of fibres which innervate the latter muscle (*r.m.r.m.o.*).

A short distance caudal to this point, a branch is given off which makes its way peripherad (*r.m.p.d.p.,s.*) in a winding course between m. retractor mucosae oris and m. cranio-basalis, and between the latter and m. protractor cartilaginis basalis anterior, and between the two protractors for the basal cartilage, and finally between m. protractor cartilaginis basalis ant. and m. protractor dentium sup. (In certain specimens the branch does not pass between the two protractors for the basal cartilage but pierces m. protractor cartilaginis basalis ant.) M. protractor dentium sup. is innervated by a bundle of fibres running rostrad. On the medial side of the common surface of m. protractor

dentium sup. and the lateral head on m. protractor dentium prof. the rest of the nerve branch divides into one bundle of fibres running caudad and one running rostrad. The caudal one runs between the two last mentioned muscles and innervate the lateral head of m. protractor dentium prof. The rostral bundle of fibres runs over to the medial side of the lateral head of m. protractor dentium prof. and innervates the head, after which the rest of the bundle innervates the medial head of m. protractor dentium prof.

After the branch has been given off to mm. protractores dentium, the mixed nerve trunk takes up a more medial course along the dorsal side of m. retractor mucosae oris. Further caudally, the nerve reaches the region where the medium paired basal plates and the unpaired caudal basal plate meet, and sends off (*sens., r.tend.*) thereby the loop-shaped branch described above (p. 343). The rest of the nerve is purely motor and only its proximal part is shown in fig. 15 (*r.m.t.,c.,p.*). This nerve runs caudad, dorsal to the lateral wall of the gutter-shaped caudal basal plate, continues further distally in a caudal and somewhat medial direction and runs dorsal to the tendon of m. clavatus into the tubular muscle. Here a branch is sent off ventrad past the rostral "orifice" of the m. tubulatus. The branch passes lateral to the tendon of m. clavatus, attains a position on the inner side of the ventral wall of the tubular muscle and bends off caudad, passing ventral to m. clavatus. The branch maintains this position relative to the muscles during the rest of its caudal course towards the caudal end of m. tubulatus, sending out branches through the ventro-medial line of m. tubulatus. These branches bend dorso-laterad and follow the outer surface of m. tubulatus, innervating the muscle.

The description of the main trunk was broken off at a point where the nerve lies dorsal to the tendon of m. clavatus and ventral to the dorsal wall of m. tubulatus. The trunk maintains this position relative to the musculature during its continued caudal course. The nerve joins its antimere from the other half of the body and gives off, at several places, branches which run dorsad through the dorso-medial line of m. tubulatus and bend off ventro-laterad on the outside of the muscle and innervate the muscle. In the caudal part of the pharyngeal roll, the nerve trunk lies up against m. perpendicularis and probably innervates it—the innervation is difficult to observe. The rest of the nerve alters its direction to ventro-caudal and divides again into a nerve for each half of the body. This nerve runs between m. perpendicularis (medially) and m. clavatus, innervating m. clavatus.

Rr. musculares velares (fig. 15, *rr.m.v.*). From the medial surface of the common, motor trigeminal root emerge some small bundles of fibres to m. craniovelaris. They ramify in the muscle. In addition the common motor root gives off a larger nerve caudad. This nerve runs along the dorsal side of m. craniovelaris, ventral to the posterior connection between the dorsal longitudinal bar and the trabecle and, also, ventral to the connection between

the dorsal longitudinal bar and the auditory capsule. The nerve divides into a medial branch (*r.m.c.v.*), which continues along the dorsal side of m. craniovelaris innervating the muscle, and a lateral branch (*r.m.sp.v.*), which runs to m. spinovelaris and follows the dorsal side of the muscle caudad, innervating the muscle.

P. FÜRBRINGER describes (1875) the nerves to the velar musculature and m. flexor trabeculae as common nerves, "rr. musculares" of "r. maxillaris externus medius". This description does not fit the present material.

Summary (cf. also p. 341). The sensory trigeminal branches running ventro-caudad, (rr. velobuccales and r. dentalis) pass through the subocular fenestra and run medial to rr. musculares. The sensory branches all run close to the wall of the buccal cavity. A number of small branches (rr. velobuccales) innervate the mucous membrane of the dorso-lateral wall of the buccal cavity between the region below the eye and the caudal orifice of the naso-hypophysial duct, the mucous membrane in the wall of the buccal cavity lateral to the velum and the mucous membrane on the velum. Finally, a branch of rr. velobuccales unites with r. muscularis posterior into a mixed trunk. From this trunk are innervated certain muscles and the mucous membrane of the ventral wall of the buccal cavity, caudal to the dental plate. In addition, a branch of uncertain character runs out into the tendon of m. clavatus. R. dentalis innervates the dental plate and the mucous membrane (skin) rostral to this plate in the ventro-lateral region of the mouth opening. A bundle of fibres from the V_2-ganglion runs lateral to rr. musculares and unites with r.m. craniobasalis. The nerve, which is thus mixed, gives off bundles which innervate m. cranio-basalis and bundles which are lost ventral to the medium paired basal plates and along the inside of the lateral wall of the gutter-shaped unpaired caudal basal plate. The character of the fibres which are thus lost in the vicinity of the basal plates is uncertain. One may suppose that they are proprioceptive, visceral afferent or autonomic.

Rr. musculares innervate all the trigeminal muscles. The nerves pass through the subocular fenestra and run—corresponding to the position of the muscles in the body—lateral to r. palatinus and branches destined for the mucous membrane of the buccal cavity, but medial to the branches destined for the skin. R. muscularis anterior runs medial to the cornual cartilage—except for the basal part of the cartilage—and chiefly medial to the labial cartilage. Branches to the laterally lying musculature run partly dorsal to the cornual cartilage, partly in the space between the base of the cornual cartilage and the base of the labial cartilage, and partly ventral to the labial cartilage.

Literature on Bdellostoma (cf. also p. 341). ALLIS states (1903) that r.m. levator cartilaginis basalis in Bdellostoma ran in one specimen dorsal to r. tentaculi IV, in another specimen through this sensory branch. (On p. 273 ALLIS seems to have used the nomenclature erroneously, as he

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mentions m. levator cartilaginis basalis as "m. quadratopalatinus", whereas on p. 275 he uses the then prevalent name for the muscle, "m. copulopalatinus".) The present author has found a variation in the relations between these nerves also in Myxine. As a rule, r.m. levator cartilaginis basalis runs dorsal to the whole of r. externus, but in one specimen the motor nerve runs instead ventral to r. externus (p. 348). In this aberrant specimen, a branch of r. externus makes its way to the skin from an origin considerably more proximal than is normal (p. 339). One gets the impression that r.m. levator cartilaginis basalis normally has a unitive effect on the externus nerve. When this unitive effect no longer exists in an aberrant specimen, r. externus starts to ramify nearer the ganglion. (The present author cannot ascertain the real causal connections.)

The variation in the relation between r. dentalis and m. flexor trabeculae described on p. 344 was also observed by ALLIS (1903) on Bdellostoma material.

The innervation of m. cranio-basalis and m. retractor mucosae oris and the branches here called rr. musculares velares and rr. velobuccales have been described differently in different papers on Bdellostoma (MÜLLER, 1839, ALLIS, 1903, WORTHINGTON, 1906). Detailed discussion on the subject is not likely to lead to anything of value as the present writer has not had access to adult Bdellostoma material. The descriptions of r. dentalis in Bdellostoma (MÜLLER and WORTHINGTON) fit on the whole the conditions in Myxine. The mixed trunk, which arises in Myxine by the uniting of r. muscularis posterior and a branch from rr. velobuccales, has its parallel in "r. lingualis" according to MÜLLER and "the posterior branch of r. mandibularis posterior" in WORTHINGTON's paper. The differences between Myxine and Bdellostoma do not appear to be large as regards this mixed nerve. (M. cranio-basalis is innervated by this nerve according to WORTHINGTON.) The present author is not able to confirm AYERS's statement (1921) that the "mandibularis nerve" has a branch which runs to the skin.

In concluding this discussion of the important similarities and differences between Myxine and Bdellostoma—Bdellostoma as described in the literature—it must be pointed out that ALLIS's data on Bdellostoma agree well with the observations made on the present Myxine material. The same variations in relations between the nerves and between the nerves and the muscles as described by ALLIS in Bdellostoma, have been found by the present author in Myxine, and he takes them as a criterion that ALLIS's account is correct and that the peripheral course of the trigeminus in Bdellostoma is almost identical with that in Myxine. Further arguments in support of this are given p. 330. On the whole, however, the literature on Bdellostoma is very confusing because of the contradictory statements made by the various writers.

It is of special interest that ALLIS stresses the individuality of the motor trigeminal nerves in relation to the sensory nerves, whereas WORTHINGTON

(1906) accounts for several mixed nerves. In the region where ALLIS's investigation is incomplete there are, however, two instances of mixed nerves in Myxine. One is the nerve originating in r. muscularis posterior and a branch of rr. velobuccales. The other is the mixed nerve formed by r.m. cranio-basalis and a bundle of fibres from the lateral part of the ganglion. In both cases the continuity between the bundles, coming from the ganglion and certain specified branches leaving the mixed nerve further distally seems established, as the calibre of the fibres in the proximal bundles and the distal branches is obviously smaller than that of the nerves ending in muscles. ALLIS supplemented his anatomic investigations with electrical stimulation of certain nerves and succeeded in proving that the motor root contains all the motor trigeminus fibres to the skeletal musculature.

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C. Nasal Duct, Naso-Hypophysial Duct and R. Palatinus.

v. KUPFFER (1893—1900) described an ophthalmic ganglion and a maxillo-mandibular ganglion and a number of smaller "epibranchial" trigeminal ganglia in embryonic Bdellostoma. v. KUPFFER was of the opinion that the "epibranchial" ganglia were serial homologous with similar ganglia further caudally and that they formed together a visceral system. ALLIS (1903) identified certain of these epibranchial ganglia and the nerves leaving them with part of the V_2-ganglion and r. palatinus in adult Bdellostoma. He considered that the presumably visceral sensory character of the ganglia in the embryo spoke in favour of a homology between r. palatinus in Bdellostoma and r. palatinus facialis in Amia. The identification of certain embryonic nerve elements with r. palatinus in adult Bdellostoma, suggested by ALLIS, is certainly correct, even if some details are open to argument. One cannot, however, draw the conclusion that r. palatinus is visceral sensory. v. KUPFFER points out himself that some of the epibranchial ganglia in Bdellostoma and Petromyzon develop into lateralis elements.

The question naturally arises as to whether the embryonic development of the peripheral region where the palatinus nerve ends can cast some light on the problem. We know from PRICE (1897) and v. KUPFFER (1893—1900, 1900) that the nasal capsule and the naso-hypophysial duct are modelled out of "the cranial and visceral ectodermal surfaces" (ALLIS, 1931 a, 1938) dorsal to the ectodermal buccal invagination. It is possible that entodermal structures also take part in the development of the naso-hypophysial duct; nothing is definitely known about this, however, as the bucco-pharyngeal plate disappears at an early stage and its position cannot be traced in later stages (v. KUPFFER, 1893—1900). We know less regarding the development of the nasal duct. A "sekundäre Rachenhaut" develops, however, and in v. KUPFFER's stage E VIII

shuts off terminally both the buccal cavity and the combined nasal and hypophysial cavity from the outside. If we compare this stage with older stages—e.g. the older of the Bdellostoma embryos decribed by v. KUPFFER (1900, fig. 1), NEUMAYER's Bdellostoma stage II (1938, fig. 7), HOLMGREN's younger Myxine embryo (1946) and the stages of Bdellostoma described in the present work (fig. 1)—it is clear that the fundamental features of the development of the nasal duct are known. v. KUPFFER (1900), v. WIHJE (1931) and STENSIÖ (1932) discuss this problem, and the following description is chiefly a combination of their statements. The distance between the most terminal part of the snout (the future mouth and nasal openings) and the nasal capsule appears to increase during certain stages in the embryonic development by a process similar to the enlargement of the "upper lip" in Petromyzon. This process affects chiefly the "archipalate" (v. KUPFFER, 1893—1900, fig 45), i.e. the area in which the subnasal cartilage and the muscles connected to it develop. The final result of the process is an embryo in which the snout —unlike the snout of the adult— points ventrad (figs. 1—3). At v. KUPFFER's stage E VIII, the combined nasal and hypophysial cavity opens in the buccal cavity by a short duct lying inside "die sekundäre Rachenhaut". Somewhere in the middle of the duct the lumen is occluded at a later embryonic stage, but the part of the duct nearest to the combined nasal and hypophysial cavity must lengthen as the distance between the nasal capsule and the most terminal part of the snout increases. This part of the duct finally has a new aperture, as the outer nasal aperture breaks through. There is certainly a relation between the existence of the elongated nasal duct and the existence of "die sekundäre Rachenhaut" in the Myxinids; Petromyzon lacks both.

Study of r. palatinus in adult Myxine supplements the known embryonic data, because the peripheral distribution of the nerve points to an affinity between the nasal duct, the naso-hypophysial duct and the dorsal wall of the buccal cavity (at least the rostral part of the latter). Bearing in mind what is known on the embryonic development of the nasal duct and the naso-hypophysial duct, it seems unlikely that the epithelium in these cavities is chiefly entodermal in origin. On the other hand, we cannot entirely rule out the possibility that the epithelium may be completely ectodermal. The conclusions which can be drawn from this argue against ALLIS's view (1903) that r. palatinus is visceral sensory. Investigations of the central connections of the nerve and the possible existence of end buds in the Myxinids are discussed in chapter XI.

D. The Grouping of the V_2-Complex.

HOLMGREN (1942 a, 1946) points out the existence of a palato-quadrat in the Myxine embryo (rudimentary in the adult) and makes a comparison between the tooth plate cartilage in Myxine and the mandibularis complex

in Holocephali and Antiarchi. Even if the similarities between the mandibular archs of the Agnathes and the Gnathostomes had not existed, there would still be reason for trying to trace a division of the V_2-branches of the Cyclostomes into maxillaris branches and mandibularis branches. The existense of such a division may be caused by the position of the branches relative to the mouth opening and the buccal cavity.

R. palatinus is presumably a maxillaris branch, as is indicated by its extension in the medial roof of the buccal cavity and in the medial structures dorsal to this. The maxillaris character of r. externus is more questionable, but may possibly be considered established by DEAN's (1899) investigation of Bdellostoma embryos. DEAN shows that all the tentacles develop dorsal to the stomodaeum, at early embryonic stages, and in tentacles I, III and IV we find the most important peripheral region of the nerve. DEAN and STOCKARD (1906) state that the dental plate of the earliest embryonic stages in which it could be observed, lies ventral to the stomodaeum. This may possibly be said to be proof that r. dentalis is a mandibularis branch, a view also established by HOLMGREN's comparison between the tooth plate cartilage and the mandibularis complex in certain other groups of fishes. The same arguments support the view that the branches of r. muscularis posterior innervating the musculature of the dental plate are mandibularis branches.

The present writer considers it impossible to subdivide the other V_2-branches into maxillaris and mandibularis branches. This discussion of the grouping of the V_2-complex is continued in chapter XII : 3.

2. N. BUCCALIS.

P. FÜRBRINGER (1875) called this nerve "r. cutan. sup. post." of n. ophthalmicus.

The root of the nerve (fig. 9, *buc.r.*) leaves the medulla dorsal to the rostral part of the utricular ganglion. The root is separated from the trigeminal roots. It runs rostrad, partly embedded in the fibrous brain capsule. Here the root runs dorsal to the utricular ganglion and reaches its own ganglion. In adult Myxine, ganglion buccalis lies entirely rostral to ganglion utricularis. Only in certain specimens is it possible to find the most anterior part of the utricular ganglion and the most posterior part of the buccalis ganglion on the same cross-section. The buccalis ganglion lies caudo-lateral to the trigeminal ganglia (fig. 8). In the smallest specimen examined (43 mm) and in one older specimen, a boundary can be seen between the buccalis ganglion and the trigeminal ganglia; in the other larger specimens the buccalis ganglion can no longer be delimited from the trigeminal ganglia. (For this reason the buccalis ganglion could not be drawn in fig. 9 between the buccalis root and the peripheral buccalis nerve.) The nerve leaves the ganglion and runs latero-rostrad. It pierces the spinal

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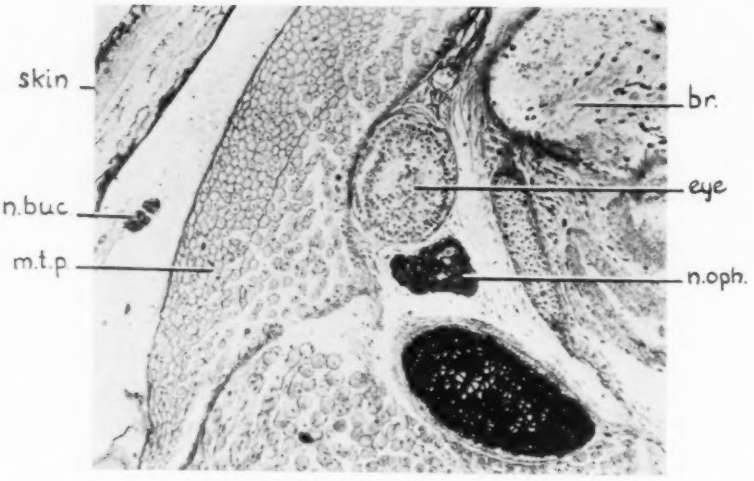

Fig. 16. Myxine, adult. Position of the eye. "N.buc." indicates a complex formed by n. buccalis and *n. oph. I.* Transverse section. 75 ×.

musculature and continues rostrad, lateral to the most caudal part of m. tentacularis posterior, and, further rostrally, enters the subcutis and spreads out there like a fan.

Discussion. ALLIS (1903) points out the difficulty of homologizing n. buccalis in Bdellostoma with the corresponding nerve in Myxine as given in P. FÜRBRINGER's description (1875). In Bdellostoma the nerve runs ventral to the eye "and hence necessarily ventral or posterior to the nervus opticus" (ALLIS, p. 271), while FÜRBRINGER is said to have drawn the corresponding nerve dorsal to n. opticus in Myxine. In Myxine, however, n. buccalis has no close relation to the opticus and the eye, since the eye does not reach the subcutis but is covered by m. tentacularis posterior (fig. 16). N. buccalis runs lateral to m. tentacularis posterior. In Bdellostoma the eye reaches the skin (cf. AYERS, 1894).

Investigations of the medulla in the Myxinids have shown that the buccalis contains both a lateralis component and a general cutaneous component (Myxine: HOLMGREN, 1919, JANSEN, 1930. Bdellostoma: AYERS—WORTHINGTON, 1908 b). According to AYERS—WORTHINGTON (1911) n. buccalis has in addition a fasciculus communis component. This component is discussed in chapter XI: 1. The existence of a lateralis component in the ophthalmicus and facialis in Myxine has been questioned (see these nerves). Myxine has a lateralis component in the glossopharyngeus-vagus complex (HOLMGREN, JANSEN). According to AYERS—WORTHINGTON (1908 b), Bdellostoma has, apart from n. buccalis, lateralis elements in the trigeminus—whether they enter n. ophthalmicus or r. externus is not clear—and probably also in n. facialis. In

addition, Bdellostoma has, according to the same authors, a n. lateralis posterior carrying exclusively lateralis fibres.

ALLIS (1903) was the first to use the name buccalis ("buccalis lateralis") for the nerve. The course of the nerve and the general distribution of the lateralis component on the cranial nerves do not argue against such a homologizing. It is, however, doubtful whether the nerve is to be reckoned as a trigeminal or facial nerve. WORTHINGTON (1906) says that in Bdellostoma the nerve is "free from all entangling alliances" with the trigeminus and the facialis but has "close contact" with the trigeminal ganglion. Since AYERS—WORTHINGTON (1908 b, Bdellostoma) discovered that the nerve also contains a general cutaneous component, they interpreted the nerve as "the posterior trunk of the trigeminus". ALLIS (1903, Bdellostoma) is certain of the individuality of the nerve, but does not exclude the possibility that it receives fibres from the "maxillo-mandibularis" complex. The embryonic development of Bdellostoma shows that the nerve is formed independently of both the trigeminus and the facialis (p. 328). The data given above regarding the conditions in adult Myxine confirm that the contact with the trigeminal ganglion is secondary. The existence of a general cutaneous component in the nerve is scarcely sufficient reason for abandoning the name n. buccalis, which seems to the present writer to be the most suitable one in the light of our present knowledge.

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3. N. FACIALIS.

N. facialis (fig. 9, *VII*) leaves the brain with two more or less separate roots; one is dorsal, the other ventral. On the present material it is not possible to decide whether some facialis fibres, as ALLIS suggests (1903, Bdellostoma), have their cell bodies embedded in the utricular ganglion. In any case, most of the facialis fibres pierce the utricular ganglion in the most caudal part of the latter. Immediately lateral to the utricular ganglion all the facialis fibres unite. In some specimens an independent facial ganglion can be observed here (fig. 17), in others it is lacking. If the ganglion exists, it is made up of only a few cells. The facial nerve runs ventro-caudad, down through a little skeletal fenestra lying caudal to the posterior connection between the trabecle and the dorsal longitudinal bar (see HOLMGREN, 1946). The nerve continues ventro-caudad along the venro-lateral surface of the auditory capsule. Here, JANSEN (1930) and others observed a ganglion, but there is no such ganglion in the present material. The nerve runs caudad and laterad and passes dorsal to a fold in the digestive tract, a fold lying lateral to the velum. When the hyo-mandibular branchial pocket is reduced during the embryonic development of Bdellostoma, its final remnants disappear in the dorsal part of this fold (STOCKARD, 1906). The mucous membrane of the digestive tract in Myxine

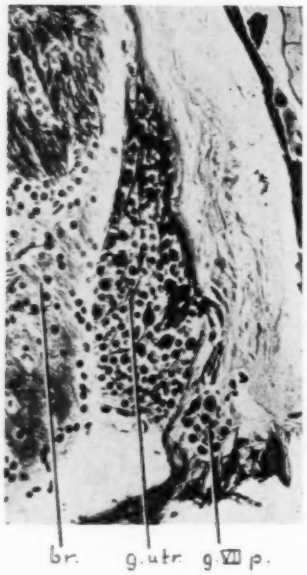

Fig. 17.

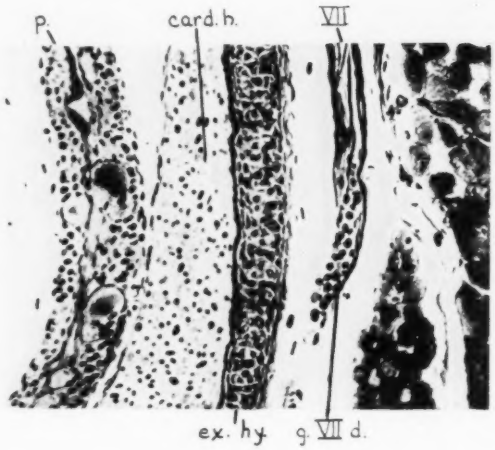

Fig. 18.

Fig. 17. Myxine, adult. The proximal facial ganglion. Note the peripheral cell bodies in the spinal nerve in the upper right corner of the photo. Transverse section. 130 ×.

Fig. 18. Myxine, adult. The distal facial ganglion. Transverse section. 130 ×.

does not appear to be innervated by the facialis either in this or any other region.

Further distally, the nerve makes a sharp bend and runs ventrad. Bundles of fibres are sent off caudad from this bend (fig. 9, *r.m.c.h*) and innervate m. cranio-hyoideus. During its ventral course the main trunk lies along the rostral edge of m. cranio-hyoideus, and a number of cell bodies are interspersed in the nerve. This distal facial ganglion (fig. 18) lies lateral to the cardinal heart (Cole, 1926). The cardinal heart does not, however, appear to be innervated by the facialis. Further distally the facialis reaches the medial side of m. protractor cartilaginis basalis post. Here it sends off one or two bundles of fibres (fig. 9, *r.m.p.c.b.p.*) which innervate the muscle after a caudal course along its medial side. After the bundles of fibres have been given off, the facialis makes a sharp bend and continues rostrad (*r.m.p.c.b.a.* + *sens.VII*). Here the nerve runs medial to m. protractor cartilaginis basalis anterior and shifts from the dorso-caudal to the ventro-rostral boundary of the muscle, and innervate it.

In addition to motor fibres, the facialis contains some very fine fibres (fig. 19). It is probable that the fine calibre fibres belong to the cell bodies in the proximal and the distal facial ganglia; it has not been possible to prove this, however, on the present material. The fine fibres could be traced to the rostrally directed r. m. protractor cartilaginis basalis ant. Bundles with fine calibre fibres are sent off from this branch and are lost lateral and ventral to

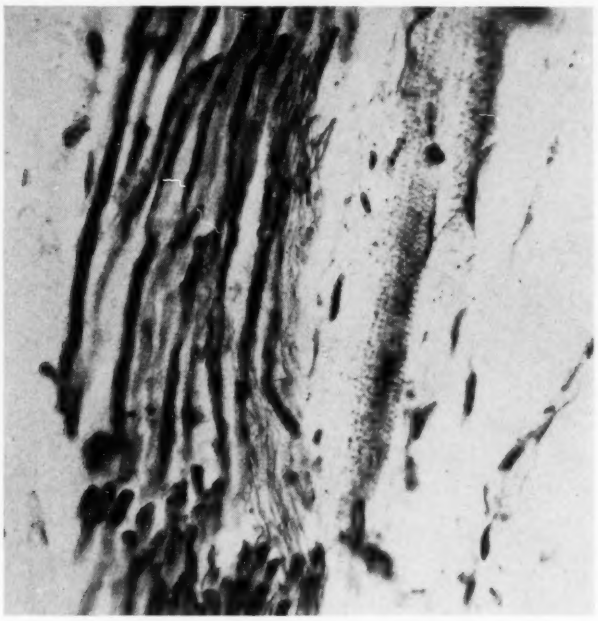

Fig. 19. Myxine, adult. Transverse section through n. facialis. Coarse and fine fibres. 380 ×.

the basal plates near the contact between the medium paired basal plates and the frontal basal plates. The destination of the fibres is thus unknown; either they innervate the lingual artery (HOLMGREN, 1946), which follows the lateral edge of the basal plates, or they are proprioceptive. The latter alternative seems more likely considering most of the fibres could be traced to a position ventral to the basal plates. In an aberrant specimen n. facialis gives off a branch consisting chiefly of fine fibres, which passes medial to r.mm. protractores dentium and contains a couple of cell bodies there. These cell bodies thus appear outside the area in which the distal facial ganglion normally occurs. The branch runs rostrad along the external side of m. protractor cartilaginis basalis ant. The fine calibre fibres could be traced to a position ventral to the basal plates.

Discussion. ALLIS (1903, Bdellostoma) found no separate facial ganglion, but WORTHINGTON (1906, Bdellostoma) states that such a ganglion always exists, but in various forms. The present writer has also found variation in Myxine, in so far as the proximal facial ganglion could not be observed in some specimens and is probably embedded in the utricular ganglion in such cases. In addition, a distal facial ganglion occurs in the present material. On the other hand no ganglion could be found at the place where JANSEN states

it ought to lie (1930). The varied nature of the facial ganglion should be clear from these data.

MÜLLER (1839, Bdellostoma and Myxine), P. FÜRBRINGER (1875, Myxine), ALLIS (1903, Bdellostoma), WORTHINGTON (1906, Bdellostoma), AYERS (1921, Bdellostoma) and NEUMAYER (1938, Bdellostoma) give accounts of the sensory branches of the facialis, based on studies of the peripheral distribution of the nerve. Their descriptions do not agree, and none of them mentions sensory branches of the nature described here. On the other hand, most of them describe a skin branch said to run laterad between m. levator cartilaginis basalis and m. protractor cartilaginis basalis anterior. One might assume that this branch contains lateralis elements in Bdellostoma and that it does not exist, or is less developed, in Myxine owing to the weak development of the lateralis system in the latter animal. HOLMGREN (1919) mentions a lateralis component in n. facialis in Myxine, but JANSEN (1930) does not confirm it. AYERS—WORTHINGTON (1908 b) consider the existence of lateralis fibres in the facialis in Bdellostoma to be likely. The question is, however, complicated by JANSEN (1930, p. 449), who describes some facialis fibres in the medulla of Myxine which run "straight medially among the descending fifth fibers, where they are lost". (Cf. also RÖTHIG, 1914.) It must, however, be stressed that no skin branches are given off from the facialis in the present Myxine material.

Earlier authors agree better on the existence of a visceral sensory component in n. facialis in the Myxinids. Such a component has been mentioned by HOLMGREN (1919, Myxine), JANSEN (1930, Myxine) and AYERS—WORTHINGTON (1911, Bdellostoma), all of whom studied the medulla. It is theoretically possible that the visceral sensory component in the facialis comes from muscle sense organs via the thick facialis fibres (and possibly via the facialis ganglia). If this is the case, the fibres must be reduced in calibre in the medulla, because HOLMGREN and JANSEN state that the sensory facialis fibres in the medulla of Myxine are fine in calibre. As, however, no proprioceptive component from the trigeminal musculature joins the fasciculus communis system in the medulla, this solution of the problem seems unlikely. Since the visceral sensory fibres, described by HOLMGREN and JANSEN, are fine in the medulla and since they are probably the only sensory facialis fibres in Myxine, one can assume that they are identical with the peripheral, finely calibred fibres and that they belong to the cell bodies of the facial ganglia. The fibres may come from blood vessels. If they on the other hand are proprioceptive, coming from sense organs in the connective tissue in the vicinity of the basal plates—and this appears to be most likely considering their peripheral course—there are some problems to solve. The nucleus of the proprioceptive fibres is then joined with the nucleus of the interoceptive fibres in an undifferentiated fasciculus communis nucleus. Such a topographic position of the proprioceptive

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nucleus is in itself remarkable. On the basis of HERRICK's discussion (1944), one would, moreover, expect that incoming impulses to the undifferentiated fasciculus communis system would release unspecific mass movements. What movements could be an appropriate answer to both interoceptive and proprioceptive impulses? Even if it is incorrect to accentuate the question so far, it is difficult to bring the facts of the facial nerve in Myxine in line with HERRICK's discussion.

Finally, the extracerebral position of cell bodies belonging to proprioceptive facialis fibres is slightly surprising, since the cell bodies of proprioceptive fibres are often intramedullary.

New investigations of the central connections of the facialis and of the end organs of the fine calibre fibres are desirable.

4. THE METOTIC CRANIAL NERVES.

The "glossopharyngeus" (the name r. pharyngeus of n. vagus should perhaps be more correct) in Myxine has not been studied closely in the present material. As far as the present writer is able to judge, its course agrees well with that of the corresponding nerve in Bdellostoma as described by WORTHINGTON (1906). ADDENS (1933) gives a review of the literature and an exhaustive discussion of the relevant problems.

5. THE SPINAL NERVES.

A. The Most Anterior Spinal Nerves.

These have previously been described by WORTHINGTON (1906, Bdellostoma). ALLEN's description (1917) of "two of the most cephalic spinal nerves" probably does not refer to the two most cephalic i.e. anterior spinal nerves.

The two most anterior spinal nerves are placed by WORTHINGTON in a special category as against the other spinal nerves and are called "spino-occipital" nerves. According to WORTHINGTON, the "spino-occipital" nerves lack motor and sensory rr. dorsales. WORTHINGTON's description gives the impression that the vagus runs between the dorsal and ventral roots of the "spino-occipital" nerves—a course which would considerably increase the difficulty of a comparison with Petromyzon.

Fig. 20 shows the most anterior spinal nerves in Myxine. (The figure does not do justice to the roots of the nerves.) Most anterior lies a complex (*sp.comp.*) probably consisting of the first and the second spinal nerves. The spinal nerves following behind the complex are very similar to one another. The most anterior r. ventralis in the complex (*r.v.1*) is divided into two. This

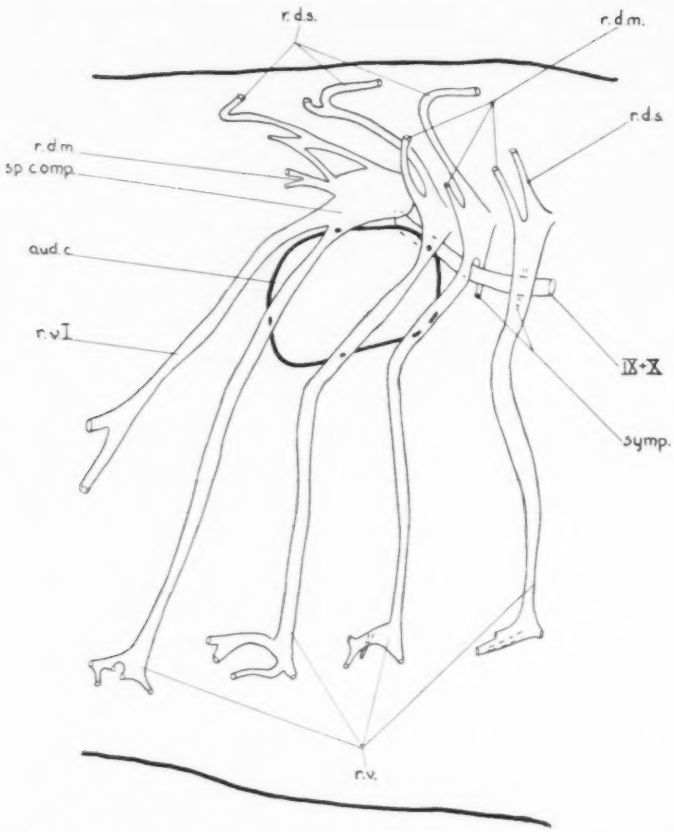

Fig. 20. Myxine, adult. Reconstruction of the anterior spinal nerves. Lateral view. 19 ×.

r. ventralis like the subsequent rr. ventrales (*r.v.*) contains fibres both from the motor root (roots) and from the ganglion (ganglia). Rr. dorsales consist of independent motor (*r.d.m.*) and sensory (*r.d.s.*) nerves, apart from some of the dorsal branches of the complex which at certain points in the peripheral course could not be distinguished from one another. Rr. dorsales of the complex consist of several motor and several sensory bundles, and one does not find here exactly the pattern which further caudally is regularly repeated. The vagus runs ventral to all the roots of the spinal nerves.

What corresponds to WORTHINGTON's two "spino-occipital" nerves is not clear, but it is probable that the above-mentioned anterior spinal complex does. It appears that the reason for separating the most anterior nerves from the rest is no longer valid and that the name "spino-occipital" should be abolished. This revaluation is justified as some of the most anterior spinal nerves in Petromyzon are compared to n. hypoglossus (p. 402). The peculiarities shown

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by the most anterior spinal nerves in Myxine should be judged in connection with the exceedingly rostral extension of the innervated skin regions and musculature, and with the "telescoping" of the medulla. The "telescoping" indicates a rostro-caudal compression of the brain in the Myxinids, as shown by RÖTHIG—ARIENS KAPPER'S (1915) and BLACK'S (1917) studies of the nuclei in the adult brain. CONEL (1929) followed this process during the embryonic development.

The anterior spinal nerve complex in Myxine has, however, one peculiarity, as part of its ganglion lies isolated, inside the meninges. This was already pointed out by JANSEN (1930). According to JANSEN, who bases his assertion on studies of the central nervous system and of the roots of the spinal nerves, the isolated part of the ganglion belongs to the first spinal nerve. The remainder of the ganglion of the complex must, therefore, belong to one or more of the subsequent spinal nerves.

It must be stressed that the end region of the spinal cutaneous nerves in the Myxinids stretches very far rostrad. This applies particularly to the skin on the ventral side. In the present material, the most anterior r. ventralis can be traced to the skin on the ventral side in the region below the nasal capsule. Immediately rostral to this point, r. externus trigemini takes over the innervation of the skin. In this the Myxinids differs markedly from the Petromyzonids.

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B. The Spinal Nerves and the Gills.

In the Myxinids the branchial region is strongly displaced caudad during the ontogenesis. Bdellostoma stouti has 10—14 gill sacs when fully grown. In this species three branchial pockets degenerate during ontogenesis according to STOCKARD (1906). A fully-grown Myxine has six gill sacs. HOLMGREN (1946, p. 68, cf. also p. 78) points out that certain characteristics in the artery system in embryonic Myxine indicate that the original number of gills in this species was the same as in Bdellostoma. In adult Myxinids a large number of spinal nerves with complete rr. dorsales and ventrales lie rostral to the branchial region. In the branchial region the ventral branches of the spinal nerves run down between the gills (v. DER HORST, 1934). All these peculiarities render a comparison to the most anterior spinal nerves and n. hypoglossus (p. 402) in Petromyzon difficult. It appears to be far more difficult to compare the spinal nerves in the branchial region of the Myxinids to those of the Gnathostomes than to make the corresponding comparison between the Petromyzonids and the Gnathostomes. This is in agreement with GOODRICH'S (1938) opinion, based on an investigation of the intersegmental arteries in the Cyclostomes. When judging the significance of the peripheral cell bodies in the spinal nerves, the comparisons discussed above should be remembered.

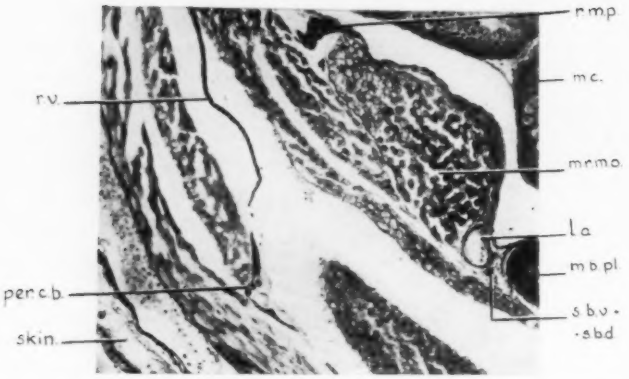

Fig. 21. Myxine, adult. Peripheral cell bodies in a r. ventralis, belonging to one of the most anterior spinal nerves. Transverse section. 55 ×.

C. Peripheral Cell Bodies in the Spinal Nerves and the Autonomic System.

Peripheral cell bodies in the spinal nerves in the Myxinids have been demonstrated by RETZIUS (1890) and ALLEN (1917). It is tempting to bring in these cell bodies when discussing the autonomic system. ALLEN is of the opinion that spinal cell bodies migrate peripherad in Bdellostoma, and that this migration may possibly be taken as a manifestation of a tendency which in the Gnathostomes gives rise to the autonomic system. ALLEN shows that the motor and sensory ventral branches of the spinal nerves are not united in the tail region in Bdellostoma. This region can thus be assumed to be rather primitive according to ALLEN. He also points out that the cell bodies in the sensory branches of the most caudal spinal ganglia are so scattered as to remind one of the diffuse arrangement of the spinal ganglia in Amphioxus. Peripheral groups of cell bodies occur, according to ALLEN, only in the caudal region and in the area in which the caudal heart lies. In the other regions ALLEN never found more than one peripheral cell body along the course of one and the same sensory or mixed spinal nerve branch. Branches containing isolated cell bodies are said to be more abundant among the rr. dorsales than among the rr. ventrales. This he took to indicate that the peripheral cell bodies do not represent an autonomic system, as they are scarce in the ventral, cranial region where there is reason to expect autonomic fibres. ALLEN also cites the occurence of cell bodies in n. vagus as a sign that a tendency to migrate also exists in other nerves. This last argument is less valid as the peripheral cell bodies in the vagus probably come from segmentally formed epibranchial ganglia (cf. v. KUPFFER, 1893—1900). There is more reason to cite

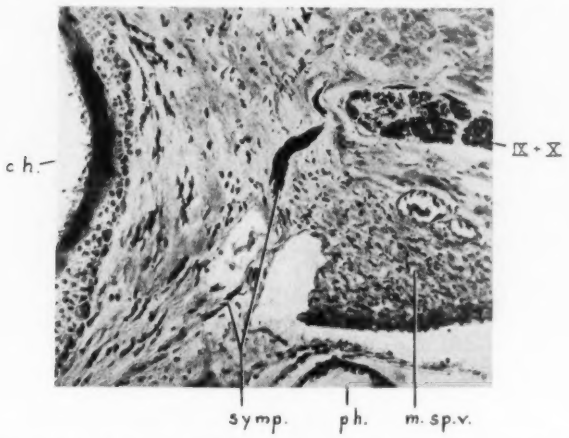

Fig. 22. Myxine, adult. Visceral branch from one of the most anterior spinal nerves. Transverse section. 95 ×.

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the varied and peripheral elongated arrangement of the facial ganglion (pp. 358 and 359).

As regards the distribution of the peripheral cell bodies, there exist groups of these cell bodies both in the dorsal and the ventral branches of the anterior spinal nerves in the present Myxine material (figs. 17, 21). These cell bodies, like the peripheral cell bodies described by ALLEN, are of the same type as the cell bodies in the ordinary spinal ganglia. The peripheral cell bodies occupy a lateral position and no connection could be observed to the digestive tract or the large vessels of the head. It is possible, but not evinced, that they are connected to the vessels and gland cells of the skin.

Certain of ALLEN's arguments are, therefore, less tenable or lack support in the nervous system of Myxine, but the rest of his discussion is sufficient to convince the present writer of the correctness of considering the peripheral spinal cell bodies in the Myxinids as being in the first place a primitive characteristic, reminiscent of the arrangement of the spinal ganglia in Amphioxus. The problem of the genesis of the autonomic system is so complicated and so far from being settled that it will not be discussed here.

Finally, it should be mentioned that some, possibly all, of the ventral branches of the anterior spinal nerves in Myxine send out thin branches (one each) which run ventrad, passing medial to n. vagus (figs. 20, 22, *symp.*). The branches are lost in the vicinity of a. vertebralis impar (COLE, 1926) and the medial dorsal wall of the pharynx between the two velar ridges. No cell bodies were observed in these branches. This shows, however, that Myxine has an autonomic or visceral afferent component in its spinal nerves.

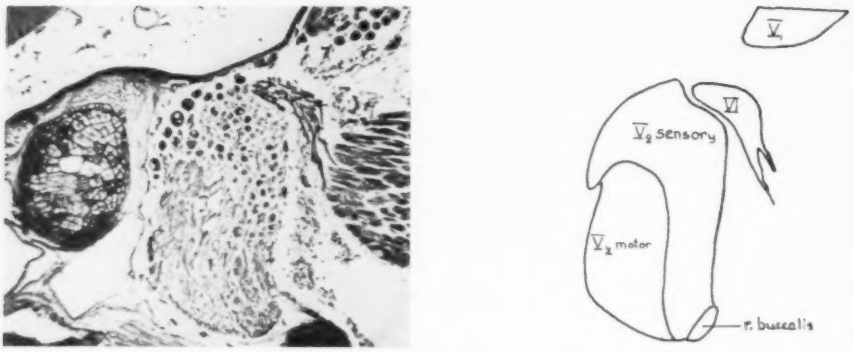

Fig. 23. Petromyzon, adult. The motor and sensory components in the V_2-complex. N. abducens runs to the orbit (right). The outlines of the components are drawn in the sketch. Transverse section. 50 ×.

VI. PETROMYZON.

The following description of the trigeminal and facial nerves will deal chiefly with the points where JOHNSTON's (1902, 1905, 1908 a) and TRETJAKOFF's (1927 a, 1929 a) descriptions disagree, or where observations made on the present material differ from both JOHNSTON's and TRETJAKOFF's. For a more detailed account of the entire course of the nerves, the reader is referred to the above papers.

1. N. TRIGEMINUS.

The description concerns P. planeri, but no significant differences were observed in the adult P. fluviatilis material (which was, however, insufficient).

The trigeminus originates from the medulla oblongata with a rostro-dorsal root (fig. 37, *Vs.r.*), and a caudo-ventral root complex. The rostro-dorsal root is common for the V_1 and V_2-ganglia. One can with TRETJAKOFF (1909 a) speak of two dorsal sensory roots—it is purely a question of how far it is possible to separate the V_1 and V_2-nerves in their central courses. The caudo-ventral complex is a motor one and consists of a little root (emerging most rostrally in the motor complex, fig. 37, *Vm.r.1*) and a strong main root (figs. 37, 39, *Vm.r.2*). The motor character of the little rostral root is not questioned by any of the writers on the subject, but it has been interpreted as a root of an eye muscle nerve (see further p. 393). TRETJAKOFF (1909 a, 1927 a) classifies the main motor root as "untere gemischte". ADDENS (1933), too, interprets it as mixed. According to JOHNSTON (1902, 1905) it is purely motor. SCHILLING (1909) and WOODBURNE (1936) are of the same opinion—the latter, however, with some reserve owing to the difficulty in making a sufficiently

close examination (cf. p. 394 in the present paper). In the present material the main motor root absorbs the little rostral motor root and the combined motor root can be traced through the V_2-ganglion. The ganglion surrounds the combined motor root medially, dorsally and laterally. The peripheral endings of the nerves issuing from the motor root lie in the trigeminal musculature (cf. fig. 40). The motor root in Petromyzon is, however, far less well delimited during its passage through the V_2-ganglion than the corresponding root in Myxine (cf. figs. 8 and 23).

A. N. Ophthalmicus (V_1).

a. *Ammocoetes.*

The ophthalmicus in Ammocoetes (profundus according to JOHNSTON, 1905, supraorbitalis according to TRETJAKOFF, 1927 a) receives a commissure from the facial ganglion. JOHNSTON states that the same commissure also carries general cutaneous fibres from the V_2-ganglion to the V_1-ganglion, but the present writer has been able neither to confirm nor to contradict this. Apart from this commissure, there are single fibres connecting the V_1- and V_2-ganglia. Their character (connections) cannot be clearly ascertained, and it is uncertain whether they occur constantly. Individual fibres and thin bundles run dorso-laterad from the ophthalmic ganglion, but the present writer has not been able to determine their peripheral endings. They are probably identical with the little branch which, according to JOHNSTON, runs dorsad and supplies two neuromasts "on the top of the head". Such a termination seems, however, improbable (cf. the adult Petromyzon). The main trunk of the ophthalmicus (fig. 24, *n.oph.*) supplies nerves during its rostral course to the nasal capsule and the skin of the dorsal side and the upper lip. The relations between the ophthalmicus and r. buccalis will be dealt with in connection with the description of the prootic lateralis nerves on page 386.

b. *The Adult Petromyzon.*

In the adult the ophthalmic ganglion receives a commissure from the facial ganglion (cf. fig. 36, *V—VII*). A second commissure was observed in one specimen between the facialis and the ophthalmicus, running lateral to the anterior part of the auditory capsule. Some thin bundles of fibres branch off from the ophthalmic ganglion and run to the skin (fig. 29, *sens.*), some passing dorsad through m. supraocularis, and some dorso-laterad. The latter run ventral to m. supraocularis but dorsal to the eye. The number of thin bundles does not appear to be constant. They correspond to TRETJAKOFF'S

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(1927 a) "rr. cutanei dorsales". Small isolated ganglia occur proximally in some of the bundles; TRETJAKOFF found similar ganglia in Ammocoetes. This should be of some significance when attempting to identify the bundles in adult Petromyzon with those in Ammocoetes, but the present author has not found such ganglia in the bundles of Ammocoetes. TRETJAKOFF states (in the table on p. 426) that the skin and supraorbital neuromasts are innervated by "rr. cutanei dorsales". The nerve bundles have, however, nothing to do with the innervation of the neuromasts. Single fibres connect the V_1 and V_2-ganglia but the abducens does not pass between the ganglia until more distally, and one can scarcely attach any significance to an interchange of fibres taking place proximal to the passage of the abducens; still more proximally the roots of V_1 and V_2 join. A certain amount of variation was observed in the courses of the thin branches joining the ophthalmicus dealt with above.

The course of the main trunk of the ophthalmicus (fig. 29, *n.oph.*) is briefly as follows. The nerve runs rostrad between the brain capsule, the eye and m. supraocularis. Only one r. etmoidalis to the nasal capsule exists (TRETJAKOFF describes two, 1927 a). Apart from this capsule, the ophthalmicus innervates the skin dorsal to the eye and that lying dorsally and dorso-laterally on the snout. In front of the nasal capsule the nerve (its branches) runs subcutaneously. The relation between the buccalis and the ophthalmicus is described on page 387.

B. The V_2-Complex.

a. *Ammocoetes.*

According to JOHNSTON (1905, p. 152) there exists in the V_2-complex in Ammocoetes a bundle of sensory root fibres which "crosses ventrad over the caudal surface of the motor root and has its ganglion cells in the ventromesial part of the ganglion". On page 153 he describes a mixed nerve, made up partly of motor fibres, partly of all the sensory fibres from the medial part of the ganglion and partly of sensory fibres from the lateral part of the ganglion. This mixed nerve gives off, according to JOHNSTON, sensory fibres to the skin in front of the longitudinal groove which connects the gill slits. The fibres correspond to TRETJAKOFF's (1927 a) r. cutaneus descendens. JOHNSTON's description gives the impression that some of the sensory root fibres pass caudal to r. mandibularis (JOHNSTON's "mesial, pure motor root") and enter the medial part of the ganglion, from whence the peripheral nerve fibres run laterad rostral to r. mandibularis. This applies, however, only partly to the present material: the peripheral nerve fibres run laterad *caudal* to the point where the motor root gives off r. mandibularis (fig. 25). Moreover,

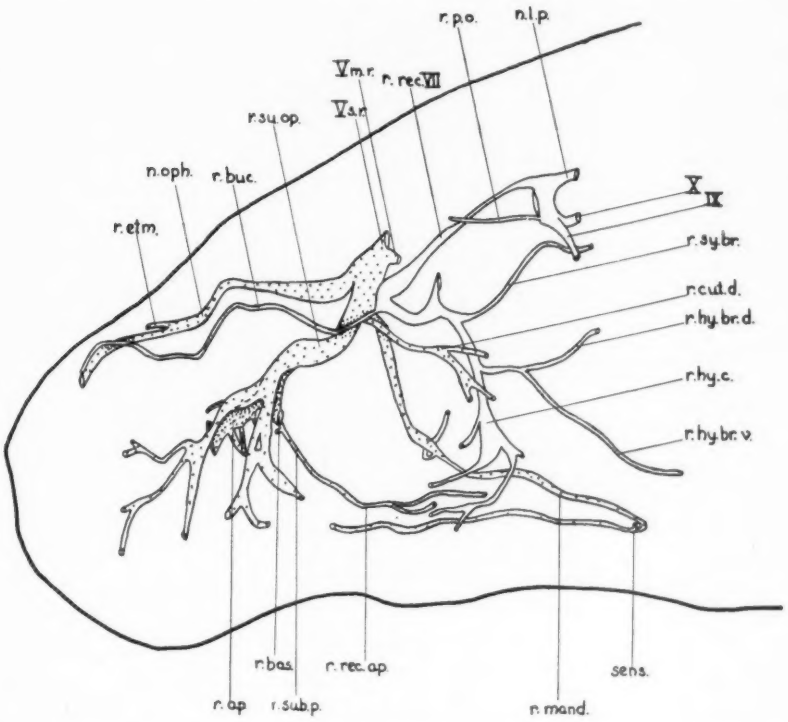

Fig. 24. Ammocoetes. Reconstruction of n. trigeminus and n. facialis. Lateral view. 25 ×.

the sensory fibres in question should probably not only be assigned to r. cutaneus descendens. Further rostrally there is another part of the V_2-ganglion medial to the motor root, but these cell bodies receive root fibres which pass the motor root on its medial side (fig. 26). These cell bodies may well be said to represent a "definitely" medial part of the V_2-complex, as against the cell bodies described above, whose connections both with the medulla and the periphery run laterad, and can therefore be said to represent a "temporary" medial part.

The commissure between the facial ganglion and the V_2-ganglion is described on page 385.

The strong motor component of r. mandibularis (fig. 24, *r.mand.*) branches off ventrad from the motor root. (JOHNSTON's name "the mesial, pure motor root" for r. mandibularis can give rise to misunderstanding. The present author has therefore preferred to use TRETJAKOFF's term, r. mandibularis. Even this name is not entirely satisfactory, as will be pointed out later.) Some fine calibre sensory fibres join the motor component in the mandibularis. In so far as it is possible to make sufficiently close observations, they come from the

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Fig. 25. Ammocoetes. The "temporary" medial part of the V_2-ganglion receives its root fibres dorsally and sends fibres out into r. cutaneus descendens. Transverse section. 260 ×.

"definitely" medial part only of the V_2-ganglion. The nerve, which is thus mixed, runs ventrad down through the velum. Rostrally and rostro-ventrally directed fibres and bundles of fibres are given off, which supply the mucous membrane of the velum with sensory nerves. The rostral surface of the velum seems to be particularly well supplied. In certain specimens these sensory fibres were collected together into a genuine branch which could be traced a long distance.

Neither TRETJAKOFF'S (1929 a) nor DAMAS' (1935) description of the velar musculature of Ammocoetes holds entirely for the present material. TRETJAKOFF'S (l.c. fig. 8) m. velohyoideus and m. velothyroideus can, however, be identified. Rostrally, the dorso-ventrally situated portions of the muscles are more or less united. Caudal to the place of joining, r. mandibularis runs from a lateral to a medial position in the external lamella of the velum. Further distally it passes to the ventral side of the velum, still medial to m. velothyroideus. The musculature and mucous membrane of the velum are innervated by a number of bundles of fibres. At the point where r. mandibularis leaves the velum ventrally and, as JOHNSTON (1905) states, bends sharply to continue rostrad, it gives off a small bundle of fibres (fig. 24, *sens.*) to the mucous membrane of the dorsad projecting, medial fold in the ventral wall of the buccal cavity (the caudal continuation of the so-called medial tentacle). TRETJAKOFF (1927 a) states that r. mandibularis divides at the bend into a rostral and a caudal (motor) branch, as is the case in adult Petromyzon. No caudal motor branch is mentioned by JOHNSTON, nor is it found in the present material. As r. mandibularis runs forward between *m. constricteur buccal* and the wall of the buccal cavity, lateral to the medial fold and to *le rétracteur des papilles*, branches are given off repeatedly to *m. constricteur buccal*. The nerve probably also innervates *le rétracteur des papilles*. R. mandibularis runs laterad,

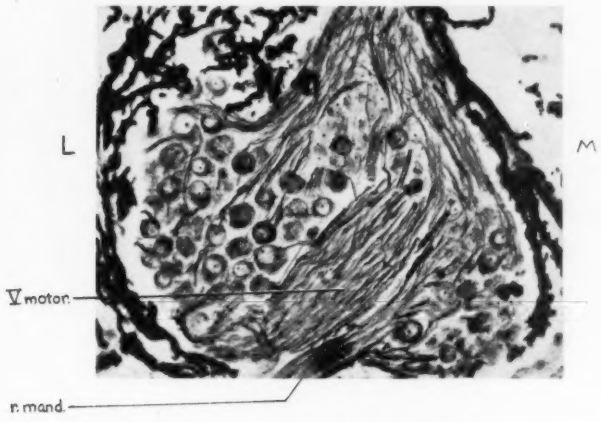

Fig. 26. The "definitely" medial part of the V_2-ganglion receives its root fibres dorsally and sends fibres out into r. mandibularis. This section lies rostral to the section given in fig. 25. Transverse section. 270 ×.

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piercing the connection between the lateral mouth plate and the ventro-lateral plate. Immediately rostral to this point the nerve splits up into terminal branches to *m. constricteur buccal.* (In some specimens the nerve may run laterad caudal to the mentioned connection.)

JOHNSTON (1905) states that r. cutaneus descendens associates itself with a motor component ("the more lateral" ramus of r. mandibularis, l.c., p. 153). TRETJAKOFF (1927 a) describes a purely sensory r. cutaneus descendens, a description which agrees with the present observations. The nerve (fig. 24, *r.cut.d.*) starts from the lateral side of the V_2-ganglion, sometimes in one bundle and sometimes in two which join, and runs lateral to vena facialis, between *m. buccal superficiel* and *la portion latérale des myomères épitrématiques* and between the latter muscle and *les myomères hypotrématiques* to the skin. The end region of the nerve lies partly (as JOHNSTON states) in the skin in front of the longitudinal groove which connects the gill slits, but also partly in the skin in the rostral part of the groove and in the skin more ventrally. The nerve joins a bundle of fibres from r. hyomandibularis (see p. 387).

JOHNSTON describes two branches from the V_2-ganglion running chiefly dorsad and says that "they are lost in myosepta on their way to the skin". Rather similar branches were observed in the present material, but they run off to the skin between *la portion dorsale et la portion laterale des myomères épitrématiques* and are lost there, caudal to the eye.

R. subopticus (JOHNSTON's "r. maxillaris") sends off r. supra-pharyngeus on its medial side (fig. 27, *r.sup.p.*). The latter nerve lies dorsally in the roof of the buccal cavity between *le rétracteur de la lèvre antérieure*

and the mucous membrane. A couple of fibres branch off dorso-laterad between the muscle and the trabecle. The destination of the fibres is unknown—they are possibly motor. All the muscles in this area are, however, innervated from elsewhere. The rest of the suprapharyngeus nerve is certainly sensory and supplies the dorsal part of the mucous membrane in the buccal cavity and the dorso-caudal part of the mucous membrane in the oral hood (DANIEL, 1933). TRETJAKOFF (1929 a) states that the nerve is mixed and supplies the *m. constricteur buccal*. JOHNSTON takes a different view as he says (1905, p. 156) that "several small branches from its" (i.e. "r. maxillaris") "chief inner branch seem to innervate pharyngeal muscles". *M. constricteur buccal* is, however, innervated by r. mandibularis.

R. subopticus runs between *m. constricteur buccal* and *la portion latérale des myomères épitrématiques*, dorsal to *m. buccal superficiel*. After sending off r. suprapharyngeus, r. subopticus (fig. 24, *r.su.op.*) divides, while continuing its rostral course, into two trunks: a lateral r. suborbitalis (fig. 24)—JOHNSTON's "outer bundle"—and a medial trunk corresponding to the apicalis-basilaris complex in the adult (figs. 24, 27)—JOHNSTON's "inner bundle". The nerve fibres issuing from the ganglion run to the sensory component of the medial trunk (which component can be identified by its fine fibres) and to r. suprapharyngeus and r. suborbitalis. The sensory fibres lie dorso-medially, dorso-laterally and ventro-laterally in r. subopticus. R. subopticus receives from the motor root a component which runs ventro-medially in the nerve. The various parts of the entire r. subopticus cannot be separated from one another with any degree of certainty, but the above description should be reasonably accurate. The peripheral distribution of the branches supports this.

Where r. subopticus divides, r. suborbitalis runs rostro-ventrad between *la portion latérale des myomères épitrématiques* and *m. buccal superficiel* to the skin passing lateral to vena facialis. Some of the terminal branches of r. suborbitalis should be specially noted; they can be traced ventrad and mediad. They follow the twisting subcutis closely, finally reaching the lower lip, the skin of which they innervate.

In the branching of the subopticus, an exclusively motor nerve is given off from the medial trunk. The motor nerve—"r. basilaris"—runs mainly ventrad and ramifies within the *m. buccal superficiel* (fig. 27, *r.bas.*). The remainder of the medial trunk—"r. apicalis"—runs rostrad and gives off r. subpharyngeus (*r.sub.p.*) on its medial side. It then gives off several bundles of fibres which innervate *le releveur de la lèvre postérieure* and *le rétracteur des papilles* (*r.m.r.l.p.*, *r.p. Le rétracteur des papilles* is, thus, doubly innervated, see r. mandibularis). These motor bundles run lateral to the lateral mouth plate.

After these motor bundles have been given off, "r. apicalis" approaches the mucous membrane of the buccal cavity (*r.ap.l*). The sensory, fine-calibre component still lies dorsal to the motor component—i.e. even in this region there exists

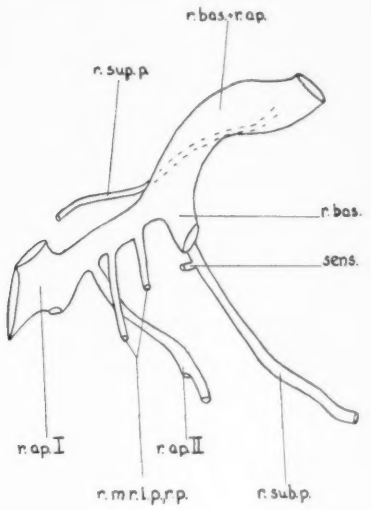

Fig. 27. Ammocoetes. Reconstruction of r. "basilaris", r. "apicalis" etc. R. suborbitalis is omitted. Lateral view. 50 ×.

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the basically important mutual relation between the sensory and motor components which was described in the ganglion region. Rostral to the lateral mouth plate, the sensory component splits into several branches to the wall of the buccal cavity and the oral hood, particularly to the tentacles, with the exception of the medial, ventral tentacle and possibly some other ventral tentacles. The motor end branches of the nerve innervate *le rétracteur de la lèvre antérieure* and *m. buccal antérieur*. One of the branches innervating the mucous membrane of the buccal cavity runs caudad, medial to the lateral mouth plate (*r.ap.II*). The innervation of *le rétracteur de la lèvre postérieure* is not clear.

R. subpharyngeus (*r.sub.p.*) is the nerve said by JOHNSTON (1905) both to innervate "the tongue" (medial tentacle) and to run a considerable distance caudad in the caudal extension of the medial tentacle. After the separation from the medial main trunk of r. subopticus, the nerve runs medio-ventrad and passes ventral to *le rétracteur de la lèvre antérieure*. The nerve clings closely to the caudal edge of the lateral mouth plate, during which course it sends off bundles of fibres which innervate the ventral wall of the buccal cavity (and possibly some latero-ventral tentacles in the oral hood). Some of these bundles run medial to the lateral mouth plate (*sens.*). R. subpharyngeus proceeds between the mucous membrane of the buccal cavity (dorsally) and the connection between the lateral mouth plate and the mucous cartilage in the medial tentacle (ventrally), turning off in a straight caudal direction innervating the mucous membrane of the medial tentacle. From roughly this point JOHNSTON's term r. recurrens can be used for the nerve. R. recurrens runs—as JOHNSTON states—laterally in the medial tentacle and its caudal extension, innervating the

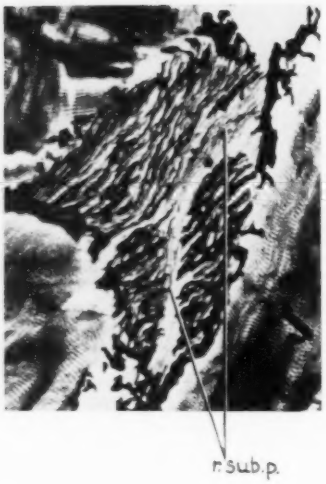

Fig. 28. Ammocoetes. Aberrant specimen. R. subpharyngeus cuts through the medial part of r. subopticus. Transverse section. 320 ×.

mucous membrane of both these structures. The nerve lies dorsal (dorsomedial) to r. mandibularis and gradually ascends higher up in the medial fold.

In one specimen r. subpharyngeus differs from the normal course (fig. 28). From its origin dorso-medially in r. subopticus, the branch runs ventrad in one half of the body *between* the motor branch of *m. buccal superficiel* and the remainder of the medial main trunk. In the other half of the body it runs as usual along the medial side of the medial main trunk. The aberrant branch behaves normally in its peripheral course.

b. *The Adult Petromyzon.*

In the adult the medial part of the V_2-ganglion is connected to the rostrad running r. suprapharyngeus and r. apicalis, to a number of small branches innervating the roof of the buccal cavity, and finally to the ventrad running r. velaris and sensory fibres in r. mandibularis (fig. 31). The lateral part of the ganglion is connected to the rostrad running r. suborbitalis and the caudoventrad running r. cutaneus descendens (fig. 29). The motor root of the trigeminus is connected to the rostrad running motor component of r. subopticus, to r. *m. tectovélaire*, to r. m. postpharyngeus and m. *vélaire descendant* and some other small branches and finally to the ventrad running r. mandibularis (fig. 31). The rostral motor component enters both r. basilaris and r. apicalis. The motor component distally to the ganglion lies between the sensory branches coming from the medial part of the ganglion and those coming from the lateral part of the ganglion. The above description is very similar to JOHNSTON's (1908 a). He states, for instance, that the motor component can be traced through the root and the ganglion out into r. mandibularis. Moreover, it is clear from his description that "the velar nerve"

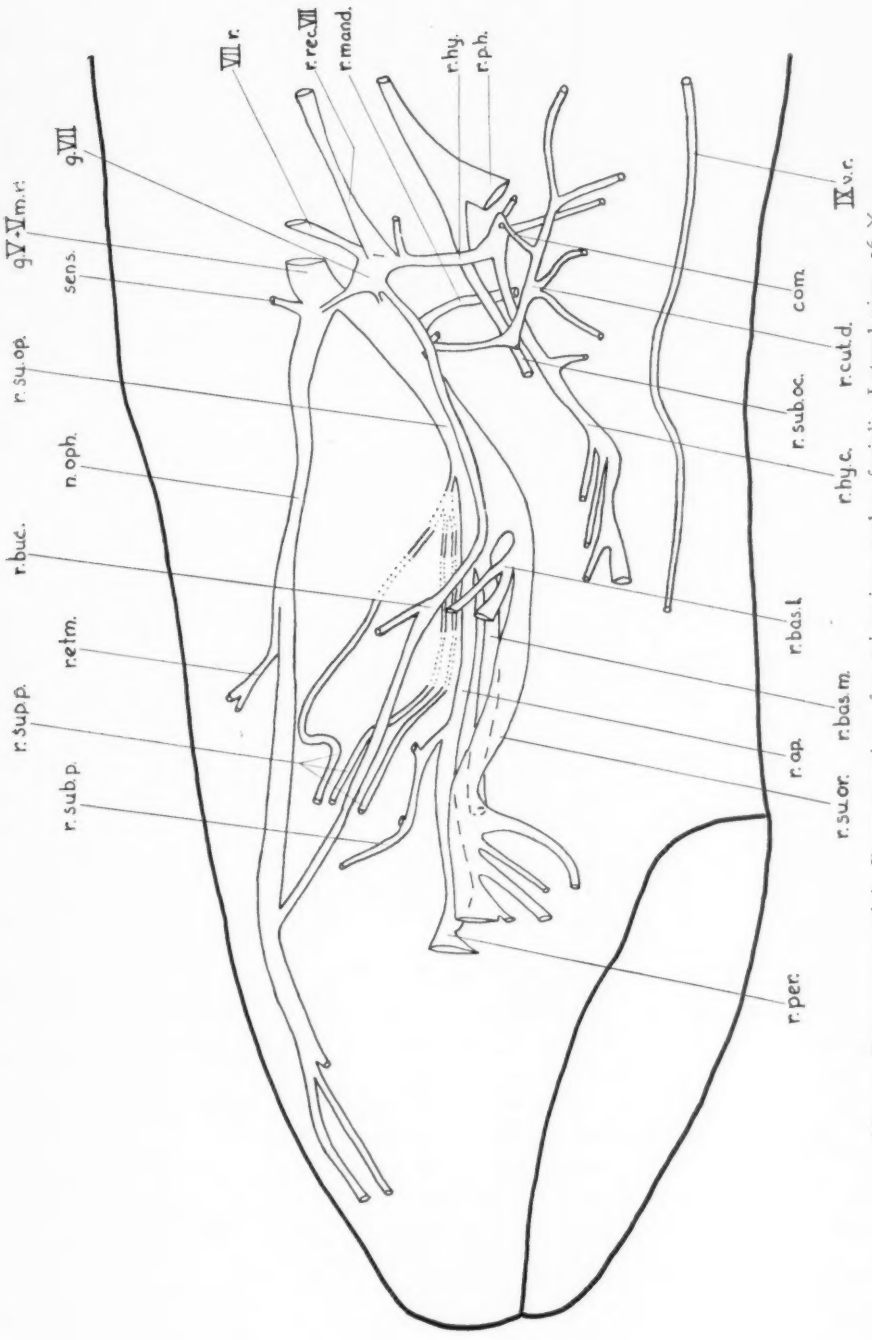

Fig. 29. Petromyzon, adult. Reconstruction of n. trigeminus and n. facialis. Lateral view. 16 ×.

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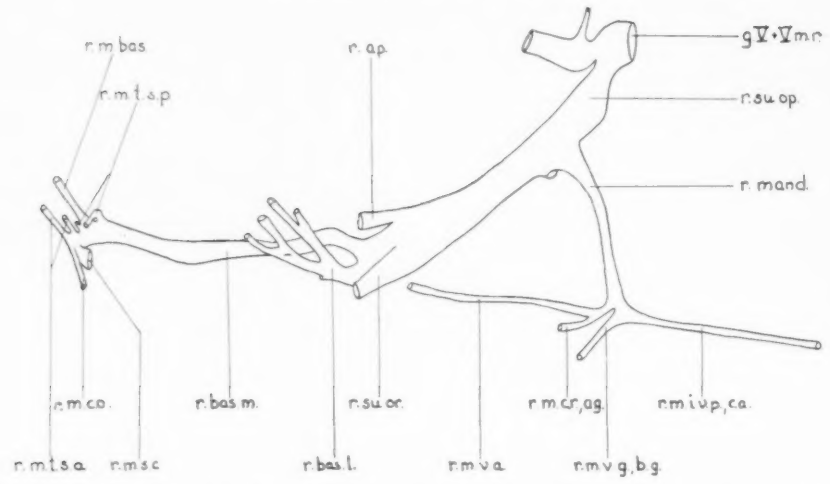

Fig. 30. Petromyzon, adult. Reconstruction of r. basilaris and r. mandibularis. Lateral view. 17 ×.

and sensory fibres to the buccal cavity run medial to the root of the mandibularis, whereas "r. maxillaris", i.e. subopticus, lies lateral to the mandibularis.

Commissures between the facial ganglion and the V_1 and V_2-ganglia, respectively, are described on page 387.

At the point where the motor root of n. trigeminus divides into two main parts, one continuing straight rostrad in r. subopticus and one running ventrad in r. mandibularis, the small motor branches mentioned above are given off. One branch, after a short rostral and medial course, reaches m. pharyngeus (fig. 31, the caudal *r.m.ph.*) which it innervates. *R. m. tectovélaire* (*r.m.t.v.*) reaches its muscle after a short, chiefly ventral course. M. velocranialis also receives nerve bundles from the motor component of the trigeminus (*r.m.v.c.*), bundles running caudal and dorsal to r. velaris. Finally, a long branch is given off ventrad: r. m. postpharyngeus and *m. vélaire descendant* (*r.m.p.p.*). This branch runs medial to r. mandibularis and divides into two —possibly more—small bundles which innervate m. postpharyngeus and *m. vélaire descendant.*

R. mandibularis (figs. 29, 30, 31, 34, *r.mand.*) is mainly derived from the motor root of the trigeminus, but also receives some fine-calibre fibres from the medial part of the V_2-ganglion. (In one specimen it also received sensory fibres from r. velaris.) As far as its sensory fibres are concerned, it seems possible to divide the ventrad running part of r. mandibularis into two regions: proximally the sensory fibres lie on the medial side of the nerve, but more distally they change over to its rostral side and spread out from there to the mucous membrane of the surface of the velum complex that faces the buccal

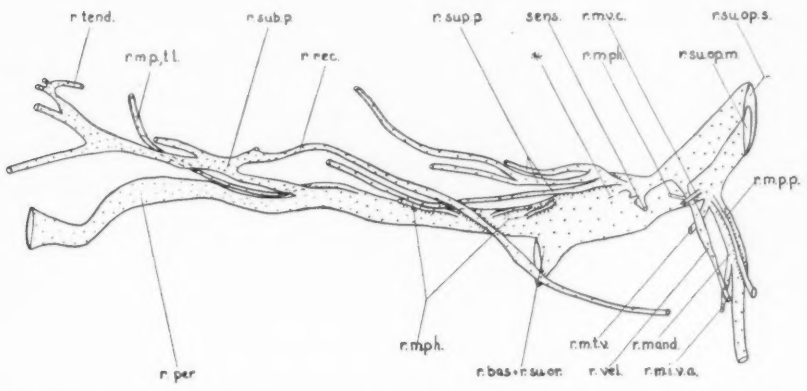

Fig. 31. Petromyzon, adult. Reconstruction of r. apicalis and some other nerves in the V_2-complex. * indicates the most distal point at which the motor and sensory components could be separated with certainty. Medial view. 15 ×.

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cavity. A thin branch from r. mandibularis innervates *m. vélaire ascendant* (fig. 31, *r.m.i.v.a.*). (According to TRETJAKOFF, 1927 a, this muscle is innervated from the "r. glossus" and not from the main trunk of r. mandibularis.) At the point where r. mandibularis ramifies, dorsal to the cornual plate, the nerve gives off a thin and very finely calibred bundle of fibres (fig. 34, *sens.*), which runs caudad up to the lateral side of *m. infravélaire postérieur* and then finally—still running caudad—continues inside the ligament attached to the ventro-lateral side of the muscle (fig. 35, *sens.*). The ventral branchial facialis bundle also occupies the same position, and it is difficult to separate the two bundles. It is not possible in the present material to find the final destination of the trigeminal bundle as the very fine fibres are lost in the ligament (cf. p. 433).

Dorsal to the cornual plate, the trunk of r. mandibularis ramifies (fig. 30). The branches destined for *m. infravélaire postérieur,* m. cardio-apicalis (*r.m.i.v.p., c.a.*), *m. vélariglosse* and m. basilariglossus (*r.m.v.g., b.g.*) cut through the cornual plate, but do not do so in exactly the same way in different specimens, nor is the number of holes through the cartilage constant. CORDS (1929 a) states that "r. posterior" does not cut through the cartilage. According to TRETJAKOFF (1927 a) the branches to *m. vélariglosse* and m. basilariglossus do not pierce the cornual plate. He combines them, together with a number of other motor branches of r. mandibularis, into a "r. glossus". There are no grounds in the present material for combining these branches into a "r. glossus". The differences, as compared with the statements of earlier writers, found in the ramifications of r. mandibularis and in the courses of its branches are such that it seems justified to attribute them to the variations of which Petromyzon appears to be capable. The specimen of

P. fluviatilis in the present material was in accordance with the above description. It only remains to mention two rostrad running branches of the mandibularis which do not pierce the cornual plate but run dorsal to it. One of them runs to *m. vélari-apical* (*r.m.v.a.*) which it innervates. The other (*r.m.c.r., a.g.*) runs between m. basilaris (laterally) and m. *vélariglosse* (medially) down to a position between m. basilaris, m. basilariglossus and the m. copuloglossus rectus—anuloglossus complex. Here, it innervates m. copuloglossus rectus and m. anuloglossus. M. copuloglossus obliquus is not—as TRETJAKOFF (1927 a) states—innervated by a branch of the mandibularis, but by r. basilaris.

R. velaris. Somewhat rostral to the point where r. mandibularis is given off by the motor root of the trigeminus, the V_2-ganglion issues a nerve on its medial side (fig. 31, *r.vel.*). The nerve—r. velaris—consists of fine fibres and runs ventrad and somewhat caudad. When it reaches m. velocranialis, it continues along the lateral side of the muscle, sending out a network of fibres ventral to the muscle. This network innervates the mucous membrane of the surface of the velum complex facing the buccal cavity. The nerve probably has nothing to do with the nerve supply of m. velocranialis, although a number of fibres pierce the muscle. The possibility that r. velaris carries some motor fibres to m. velocranialis and *m. vélaire ascendant* (see below) cannot be entirely ruled out, but, since the muscles receive nerve fibres from the ramification point of the motor component and from r. mandibularis respectively, fibres which are considerably thicker, it is probable that r. velaris is purely sensory. During its subsequent ventral course, the nerve meets *m. vélaire ascendant* which it pierces (fig. 32). At the same time the nerve splits up into single fibres. Wherever they could be followed, these fibres were found to innervate the mucous membrane of the rostral orifice of the branchial duct.

Finally, it should be mentioned that in one specimen r. velaris can be traced to the ganglion lateral to the motor root of the trigeminus. As the fibres in r. velaris are finer than the surrounding fibres the nerve could be traced a little further in a central direction, running between the motor root and the lateral part of the V_2-ganglion. It is finally lost dorsally in the V_2-ganglion.

It is not possible to find in the present material a branch of the trigeminus innervating m. cornealis (TRETJAKOFF, 1927 a: "n. cornealis"), nor a nerve originating in the V_2-complex and running via m. rectus inferior to the eye (TRETJAKOFF: "n. ciliaris").

R. cutaneus descendens (fig. 29, *r.cut.d.*) originates in the lateral part of the V_2-ganglion as one bundle or as two bundles which soon unite (varying even in the two halves of the body of the same specimen). The nerve passes ventral to r. buccalis and the subocular arch and likewise ventral to m. praebranchialis but dorsal to r. subocularis and the posterior

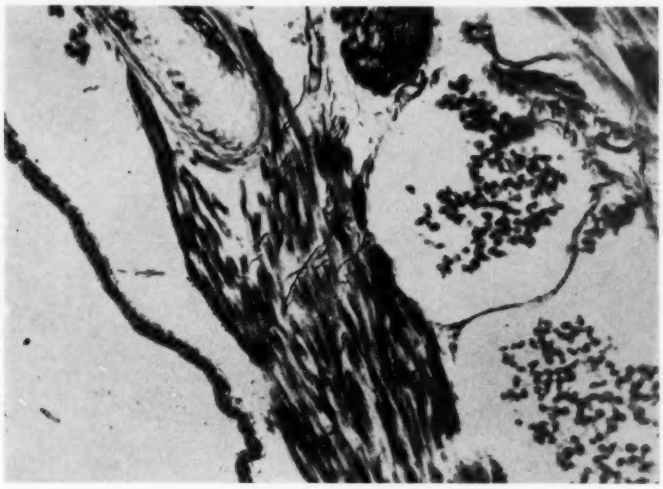

Fig. 32. Petromyzon, adult. Fibres from r. velaris, piercing *m. vélaire ascendant*. Transverse section. 175 ×.

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part of m. subocularis. TRETJAKOFF'S statement (1927 a) that r. cutaneus descendens runs dorsal to r. buccalis and the subocular arch does not, therefore, hold true for the present material. In the subcutis, the branches of the nerve spread out, fan-shaped, from ventro-rostrad to caudad. Here, thin end branches sometimes meet with branches of r. hyomandibularis, and it is difficult to separate the various elements further distad. The ramifications of r. cutaneus descendens is shown in fig. 29. Only the branch running direct caudad in fig. 29 reaches the skin rostral to the first external branchial aperture. This branch receives a contribution from r. hyomandibularis (*com.*). Normally the facialis branch is almost as thick as the branch from r. cutaneus descendens, but in aberrant specimens the facialis branch is much smaller and difficult to detect. Distal to the point where the nerves meet it is impossible to separate the facialis and trigeminus fibres in the mixed nerve. The calibre of the fibres is of no help. The terminal region of the mixed nerve is not only the skin rostral to the first branchial aperture, but also the skin a good distance ventral to it where the nerve meets with branches from the glossopharyngeus. The present writer is thus only able to define very approximately the complex of fibres reaching the neuromasts rostro-ventral to the first branchial aperture. Judging from the calibre of the fibres, the branch of the facialis, the trigeminus and the glossopharyngeus may carry lateralis fibres. The branch of the facialis and the trigeminus certainly carry, in addition, other fibres (with a finer calibre).

R. subopticus (fig. 29, *r.su.op.*). JOHNSTON states (1908 a) that branches of the "maxillaris", i.e. the subopticus, form a plexus ventrally in the

orbit and that fibres from this plexus supply the cornea and the skin in front of and behind the eye. In the present material, however, most of the nerve fibres lying ventrally in the orbit originate from r. buccalis, and only one branch of the trigeminus could be traced in this region. This branch runs caudad in the orbit to the skin. The branch originates from the V_2-ganglion itself and runs close to the cutaneous branches issuing from the facialis-trigeminus commissure. It is worthy of note that the skin between the auditory capsule and the eye and between *la portion dorsale et la portion latérale des myomères épitrématiques* mainly contains fibres originating from the V_2-ganglion in Ammocoetes, but lodges facialis branches from the VII—V commissure in the adult.

R. suborbitalis can be identified in r. subopticus as a rather well delimited portion right from the lateral part of the ganglion, apart from the fact that it has a common origin with r. cutaneus descendens. On the medial side of r. subopticus, the sensory component can be distinguished from the motor component as far as a point somewhat distal to the origin of r. supra-pharyngeus (fig. 31). The further distal the more difficult it is to separate the various components from one another. A study of a series of cross-sections gives the impression, however, that the sensory component leaves its dorso-medial position in r. subopticus and changes to the medial side of the nerve and—still more distally—to the medial side of r. apicalis, where the sensory bundle of fibres has a half-moon shaped cross-section. The way in which certain motor branches to m. pharyngeus leave r. apicalis (see below) indicates that this impression is very likely correct.

Rostral to r. velaris, a group of thin bundles of fibres is given off both rostrad and caudad from the medial part of the V_2-ganglion (fig. 31, *sens.*). (It is difficult to see why a dividing-line should be drawn between these branches and r. velaris. The present author, however, has preferred not to deviate too widely in the descriptive sections from the subdivision of the trigeminus in Petromyzon made in previous literature on the subject.) These thin bundles are destined for the dorsal wall of the buccal cavity, and are therefore most closely related to r. suprapharyngeus. In order to reach the mucous membrane of the buccal cavity, the nerve bundles must pass through the dorsal part of m. pharyngeus, and, in doing so, they are split up into smaller bundles with a few fibres each or single nerve fibres. It is particularly difficult to follow the caudal fibres as their passage through m. pharyngeus stretches over a considerable area. Under such circumstances it is imposible to state quite definitely that all the fibres are destined for the mucous membrane of the buccal cavity; on the contrary, it is very probable that single motor fibres innervate m. pharyngeus and that these motor fibres join the sensory fibres distal to the point where the latter leave the V_2-ganglion. The vast

majority of the fibres are, however, sensory, and, sooner or later, pass through the muscle to the mucous membrane.

TRETJAKOFF describes (1927 a) r. suprapharyngeus as a motor, possibly also a sensory, double-branched nerve. In the present material this nerve was particularly studied in P. planeri, as it is easier to trace in this species. The specimen of P. fluviatilis studied gives, however, no reason for assuming that r. suprapharyngeus should differ in any important respect in the two species. The nerve (fig. 31, *r.sup.p.*) originates in the medial, sensory part of r. subopticus where the latter runs ventro-medial to the orbit. R. suprapharyngeus divides almost immediately into three or more branches. These run rostrad and lie at first on the outer surface of the almost cylindrical m. pharyngeus. Further distally the nerve branches lie embedded in the muscle and finally pass over to its inner surface. The most dorsal of the branches curves dorsad (fig. 29), the curve being caused by the hydrosinus (REYNOLDS, 1933). This branch can be traced farthest rostrad. It runs past the rostral limit of m. pharyngeus along the roof of the buccal cavity, ventral to the anterior dorsal plate. The number of fibres in the branches of the suprapharyngeus gradually decreases. All the nerve fibres which could be traced are destined for the mucous membrane of the buccal cavity. M. pharyngeus, which according to TRETJAKOFF (1927 a) is innervated by r. suprapharyngeus, is on the contrary innervated by the main trunk of r. subopticus and by r. apicalis.

From r. subopticus and r. apicalis some few fibres are repeatedly sent off in bundles, which run in a central direction at a more or less sharp angle towards m. pharyngeus and ramify almost immediately after they reach the muscle (fig. 31, *r.m.ph.*). Here it often happens that the motor fibres pass close to the branches of the suprapharyngeus. It is often difficult to distinguish which fibres come from which branch, but the motor fibres are somewhat thicker and stain more intensely than the sensory fibres. Each motor fibre finally gives off very thin terminal branches, which are, on the other hand, much thinner than the fibres in the branches of r. suprapharyngeus. R. suprapharyngeus and the sensory branches mentioned on page 380, originating rostral to r. velaris, run in a way typical of sensory branches in Petromyzon, gradually dividing into smaller units. On the other hand, the supposed motor branches running to m. pharyngeus behave—with one exception—in a way that is characteristic of motor branches (cf. chapter VII). A muscle is normally innervated by *one* nerve branch, but m. pharyngeus is repeatedly innervated. This is probably due to the special shape of the muscle: it is rostro-caudally elongated and the motor trunk runs parallel to the longitudinal axis of the muscle.

According to JOHNSTON (1908 a), the ratio between the number of nerve and muscle fibres in the parietal musculature innervated by spinal branches is 1/100. The present author has attempted to estimate this ratio for some trigeminal muscles. Muscles were chosen where the result could be expected to

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be comparatively reliable viz. m. copuloglossus obliquus and *m. vélari-apical*. Here the number of nerve fibres is relatively larger, the ratio between nerve and muscle fibres being of the magnitude 1/10. Judging from these figures, it seems as if the number of motor fibres to m. pharyngeus observed by the author is an adequate number for the muscle. It is thus unnecessary to assume that r. suprapharyngeus contains motor fibres.

One peculiarity in a motor branch to m. pharyngeus should be mentioned. It was pointed out on page 380 that the sensory component from the medial part of the V_2-ganglion appears to run on the medial side of r. subopticus and r. apicalis in the region rostral to the point at which r. suprapharyngeus is given off. That this is in reality the case is supported by the fact that a motor branch from r. apicalis to m. pharyngeus does not originate at the point on r. apicalis nearest to m. pharyngeus. It starts instead from a point immediately ventral to the part of r. apicalis which, judging from the cross-sections, was presumed to carry sensory fibres.

Below the rostral part of the eye, r. subopticus divides into three nerve trunks, r. suborbitalis, r. basilaris and r. apicalis. These pass ventro-medial to the rostral part of the subocular arch.

R. suborbitalis (fig. 29, *r.su.or.*) runs rostrad and somewhat laterad to a position between m. basilaris and m. subocularis. Further rostrad m. basilaris is replaced by m. tectospinosus posterior on the medial side of the nerve. R. suborbitalis passes dorsal to m. subocularis and reaches finally a subcutaneous position. R. suborbitalis innervates chiefly the skin on the lateral side of the anterior part of the head. Moreover, it supplies certain parts of the suctorial disc, but it was not possible to fix in detail the boundary between it and the end region of r. apicalis in the suctorial disc. The anterior neuromasts in the accessory branch of "der Inframaxillar-arm" (MERKEL, 1880), i.e. the oral line (HOLMGREN, 1942 b), are innervated by fibres which, if traced in proximal direction, appear to join up with branches of the suborbitalis. Whether they join this nerve permanently or pass to branches from r. hyomandibularis, the present writer is unable to decide. HOLMGREN considers that the oral line is innervated from the facialis. It appears, however, as if the fibres from r. hyomandibularis are mainly used up for the innervation of the caudal neuromasts in the oral line.

R. basilaris divides, as TRETJAKOFF (1927 a) states, into two branches, and the lateral branch (figs. 29, 30, *r.bas.l.*) runs towards and medial to r. suborbitalis for a certain distance before it ramifies into end branches to m. basilaris. The medial branch (*r.bas.m.*) runs ventro-lateral to r. apicalis, medial to the posterior lateral plate and ventral to the ventro-caudal point of the anterior dorsal plate. Here the medial branch of r. basilaris ramifies (figs. 30, 33) and innervates m. basilaris (*r.m.bas*), m. tectospinosus anterior and posterior (*r.m.t.s.a.*, *r.m.t.s.p.*), m. spinosocopularis (*r.m.s.c.*) and m.

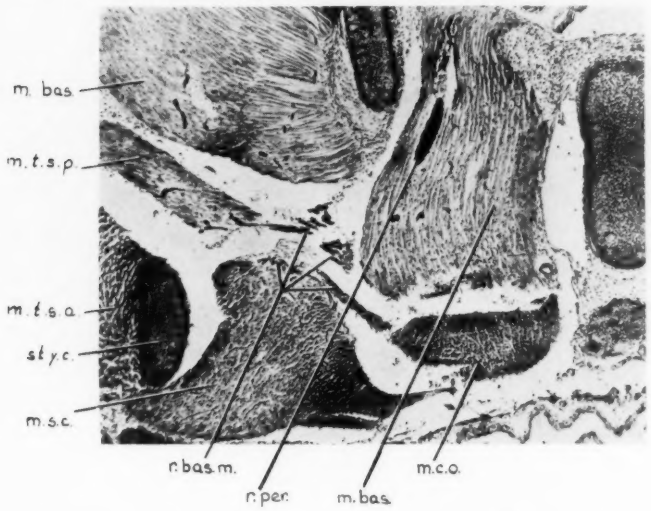

Fig. 33. Petromyzon, adult. The ramification of the medial basilaris branch. Transverse section, 55 ×.

copuloglossus obliquus (*r.m.c.o.*). According to TRETJAKOFF the last mentioned muscle is innervated by r. mandibularis.

R. apicalis (figs. 29, *r.ap.*, 31) runs rostrad along the cylindrical m. pharyngeus and lies here ventro-lateral to the muscle (in "der äussere Teil des pharyngealen Sinus", TRETJAKOFF, 1926 b). The nerve passes medial to the posterior lateral plate, and sends off r. subpharyngeus (fig. 31, *r.sub.p.*) and a motor branch (*r.m.p., t.l.*). The motor branch starts from the dorsal surface of r. apicalis, lateral to the starting point of r. subpharyngeus. Both the motor branch and r. subpharyngeus run rostrad with the motor branch most laterally. The motor branch is the most anterior and the thickest of the nerve branches which innervate m. pharyngeus. The motor branch sends out terminal fibre bundles to m. tectolateralis. R. subpharyngeus will be described below. What remains after r. apicalis has given off these branches will be called r. perforans according to TRETJAKOFF (1927 a). It runs rostrad and pierces the part of m. basilaris lying on both sides of the piston cartilage and passes ventral to the anterior lateral plate. The relation between the nerve and the ligaments anterior to the medial ventral plate is described on page 415. It should be added to TRETJAKOFF's description of the nerve that before piercing the annular cartilage, it sends off some branches with fine fibres to the mucous membrane and cornual teeth in the ventral and lateral parts of the suctorial disc. This has been described by CORDS (1929 a). However, sensory branches are given off to the suctorial disc even after r. perforans has pierced the annular

cartilage. These sensory branches innervate *inter alia* the cornual teeth situated dorsally in the suctorial disc.

R. subpharyngeus (fig. 31, *r.sub.p.*) pierces the ventral wall of the cylindrical m. pharyngeus and sends off r. recurrens (*r.rec.*) caudad, after which the nerve runs out into the lateral region of the rostral head of the piston mechanism. In addition to the sensory and motor bundles of fibres described by TRETJAKOFF as running to the piston head and to its small muscles, r. subpharyngeus has a terminal branch which (*r.tend.*), with a rather twisting course (to allow of displacements), enters from the dorsal side into the common tendon of m. cardio-apicalis and *m. vélari-apical*. The branch splits into a number of fibres which are lost in the tendon and other fibres which pass into *m. vélari-apical*. Both muscles are also innervated by r. mandibularis. STEFANELLI (1932) has described sensory nerve endings in muscles belonging to the piston mechanism. It may be supposed that the function of this subpharyngeus innervation of the muscles and their tendon is registration of the tension. The calibre of the fibres is of no assistance to the analysis of the function, as the motor and sensory fibres in r. subpharyngeus are very similar in calibre.

R. recurrens was named by P. FÜRBRINGER (1875). TRETJAKOFF (1927 a) denies the existence of the nerve. The nerve exists, however, but corresponds only partly to FÜRBRINGER's description. In stating that the nerve runs to the caudal terminus of the pharyngeal roll, innervating m. cardio-apicalis, *m. vélari-branchial* and *m. infravélaire postérieur*, FÜRBRINGER must have interpreted the retrogressive motor component of the mandibular nerve as a continuation of r. recurrens. After r. recurrens has left r. subpharyngeus it runs caudad in the lateral, and, further caudally, in the ventral wall of the buccal cavity, innervating the mucous membrane. In some specimens the nerve is divided into two bundles, in others it is single. In one specimen it was seen to pierce *m. vélari-apical*, but it normally runs dorsal to this muscle. The farthest caudal branch of the nerve lies along the ventro-medial line of the buccal cavity, dorsal to the tendon sheath of m. cardio-apicalis. In some specimens it pierces the rostral part of *m. infravélaire postéricur*. The branch finally runs into the wall of the buccal cavity along a little ridge which projects ventrad into it.

C. The Grouping of the V_2-Complex.

An attempt was made on p. 354 to subdivide the V_2-complex in Myxine into maxillaris and mandibularis branches. The reason given there also justifies a subdivision of the nerve in Petromyzon. R. suprapharyngeus possibly belongs to the maxillaris group as the nerve ramifies in the roof of the buccal cavity. R. mandibularis, which innervates the muscles ventral to the buccal cavity, may with some justification be classified as belonging to the mandibularis

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group as the muscles are partly unpaired. All other attempts to refer the trigeminal branches to a r. maxillaris or a r. mandibularis, seem for the time being to be doomed to failure. This discussion is continued in chapter XII : 3.

2. N. FACIALIS.

The facialis nerve contains, acording to JOHNSTON (1902, 1905, 1908 a), a lateralis, a general cutaneous, a visceral motor and a visceral sensory component. PEARSON (1936), WOODBURNE (1936), BARNARD (1936), STEFANELLI (1937) and HEIER (1948) confirm JOHNSTON's data.

JOHNSTON (l.c.) and TRETJAKOFF (1909 a, 1927 a) describe the roots and ganglia of the facialis in larval and adult Petromyzon. The lateralis component is said to have the most rostral roots, running through the auditory capsule unconnected with the cell bodies of ganglion prooticum. Below the auditory capsule, these roots are said to enter ganglion hypoticum. In Ammocoetes, the ganglion hypoticum is represented by two somewhat different ganglia. On the other hand, the ganglion prooticum of the other sensory fibres is said to lie inside the auditory capsule. The motor roots are said (JOHNSTON, 1905) to run between the lateralis roots and the other sensory roots of the facialis, or, (according to TRETJAKOFF, 1927 a), between the communis and the general cutaneous fibres. JOHNSTON states that the communis fibres from the ganglion prooticum make their way partly to r. sympathico-branchialis, partly to r. hyomandibularis and partly—a few fibres—to r. recurrens. These investigations were made on Golgi-treated material. In the present material the relations between the roots and ganglia of the facialis are not so clear, either in Ammocoetes or in the adult animal. The nerve bundles coming from the ganglion prooticum in the adult appear to run rostrad after emerging from the auditory capsule, but they could only be traced a short way. Most of the fibres are characterized, however, by their fine calibre, and similar fine-calibre fibres are found chiefly in r. sympathico-branchialis and in the branchial bundles of r. hyomandibularis, so that there is no reason to question JOHNSTON's data.

a. *Ammocoetes.*

In Ammocoetes, the branches of the facialis (fig. 24) are r. buccalis and the commissure to the trigeminus complex, both of which run rostrad, and r. recurrens, r. sympathico-branchialis and r. hyomandibularis, all of which run caudad proximally.

Concerning the commissure to the trigeminus complex, JOHNSTON (1905, p. 161) writes that it "is joined by fibres from the Gasserian ganglion, bends up and enters the profundus". It is difficult to trace the nerve as the region through which the commissure runs is strongly pigmented.

As a rule, in the present material, it crosses a bundle of fibres running from the V_2-ganglion to the skin caudal to the eye. It was not possible to decide whether the V_2-fibres joined the commissure or whether the commissure gave off some fibres to the V_2-ganglion. In its subsequent course the commissure passes lateral to n. trochlearis and joins the V_1-ganglion. Moreover, it should be mentioned that in one specimen the commissure is lost in the lateral part of the V_2-ganglion, while a bundle of fibres (possibly the same?) emerges further rostrally from the dorso-lateral side of the V_2-ganglion and runs up to the ophthalmic ganglion in an otherwise typical course.

R. buccalis (*r.buc.*) runs ventral to the eye, lateral to the V_2-ganglion and dorsal to *la portion latérale des myomères épitrématiques* out to the subcutis. ALCOCK (1899) states that "ophthalmicus superficialis facialis" innervates the entire row of neuromasts corresponding to "der Infraorbital-arm" in MERKEL's (1880) description (HOLMGREN's "posterior and anterior division" of the "buccalis-innervated part of the system", 1942 b) of the adult. COLE (1899) points out that the nerve should be called r. buccalis. JOHNSTON (1905) considers that r. buccalis innervates only the posterior part of the rows of neuromasts, whereas TRETJAKOFF (1927 a) states that r. buccalis in its distal course joins n. ophthalmicus. It remains to state that the joining of the two nerves is not more intimate than to allow r. buccalis to be traced as an individual bundle almost to the tip of the snout. Here r. buccalis lies lateral—dorsal to the ophthalmicus. This agrees with ALCOCK's description and with ALLIS's (1924 b) statement that all the neuromasts are innervated from the buccalis.

The present writer has not been able to determine to what extent r. recurrens (*r.rec.VII*) contributes to the innervation of the skin and neuromasts lateral to the auditory capsule. The nerve runs lateral to the auditory capsule up to the metotic ganglion complex. It was also impossible to decide whether r. sympathico-branchialis, which runs caudad along the dorsal wall of the branchial part of the gut, is sensory or motor (*r.sy.br.*). For further discussion of these questions, the reader is referred to JOHNSTON's (1905) and TRETJAKOFF's (1927 a) works.

R. hyomandibularis (TRETJAKOFF's "hyoideus") has been well described both by ALCOCK (1899) and JOHNSTON (1905). The name hyomandibularis is taken from JOHNSTON (l.c.). It is worth while, however, to point out the following. The nerve runs ventro-laterad and somewhat caudad from the ganglion along the outer side of m. constrictor praebranchialis. It passes caudal to the transverse sinus formed by vena facialis where it runs into vena mandibularis. In its course alongside m. constr. praebr., r. hyomandibularis gives off a branch caudad. This branch innervates the muscle, and gives off some scattered fibres to the mucous membrane of the branchial part of the gut near the origin of the branch. The branch then divides into two. One part (*r.hy.br.d.*) runs caudad along the inner side

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of m. constr. praebr. as far as the first external branchial aperture where it is lost. According to ALCOCK this branch is motor. The other branch (*r.hy.br.v.*) runs ventro-caudad, also along the medial side of m. constr. praebr. It passes here dorsal to m. velothyroideus (TRETJAKOFF, 1929 a), and finally runs caudad alongside the thyroidea and is then lost.

The main trunk of r. hyomandibularis continues to the skin, passing between the ventro-lateral plate and the first branchial arch. A small bundle of fibres is given off running caudad in the subcutis to the rostral part of the groove which connects the branchial apertures. Branches from r. cutaneus descendens also run through this area and the facialis and trigeminus bundles meet. (HATSCHEK, 1892, describes a so-called "trigeminus-facialis commissure".) After this branch has been given off, r. hyomandibularis (*r.hy.c.*) pierces the most anterior part of *les myomères hypotrématiques* and ramifies in the subcutis, the three most important branches running rostrad.

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b. *The Adult Petromyzon.*

The investigations were carried out on P. planeri. The facialis-trigeminus commissure and some other details were, however, studied in P. fluviatilis too.

The facialis in the adult consists of the same main parts as in Ammocoetes. TRETJAKOFF (1927 a) states that the commissure between the facialis and the trigeminus (fig. 36, *V—VII*) consists of a trunk which divides into a nerve to the ganglion ophthalmicus and a nerve to the V_2-ganglion. There are, however, in addition two or three bundles, each consisting of two or three fibres (*V—VIIcut.*), which are given off from the commissure and run caudal to m. obliquus posterior to the skin in the area between m. supraocularis and m. praebranchialis.

Contrary to TRETJAKOFF's (l.c.) statement, r. buccalis (figs. 29, 36, *r.buc.*) runs dorsal to r. cutaneus descendens (both in P. planeri and in P. fluviatilis). During its passage through the orbit, r. buccalis gives off 4 to 5 thin bundles of fibres passing dorsal to the horizontal part of the subocular arch and ventral to the eye and running laterad to the skin. They are lost in the skin ventral to the eye. The main trunk of r. buccalis also runs dorsal to the horizontal part of the subocular arch and lateral to the V_2-ganglion, then passes dorsal to m. praebranchialis out to the subcutis. It innervates the neuromasts ventral and rostral to the eye (the caudal part of "der Infraorbitalarm", MERKEL, 1880). Further rostrally r. buccalis and r. ophthalmicus unite, but not more intimately than to enable the buccalis to be traced further to the lateral and dorsal sides of the ophthalmicus. Even after r. ophthalmicus has divided into several main trunks, the buccalis lies nearest the epithelium at the points where the buccalis crosses one of the main trunks of the ophthalmicus. The possibility of an exchange of fibres between the buccalis and the oph-

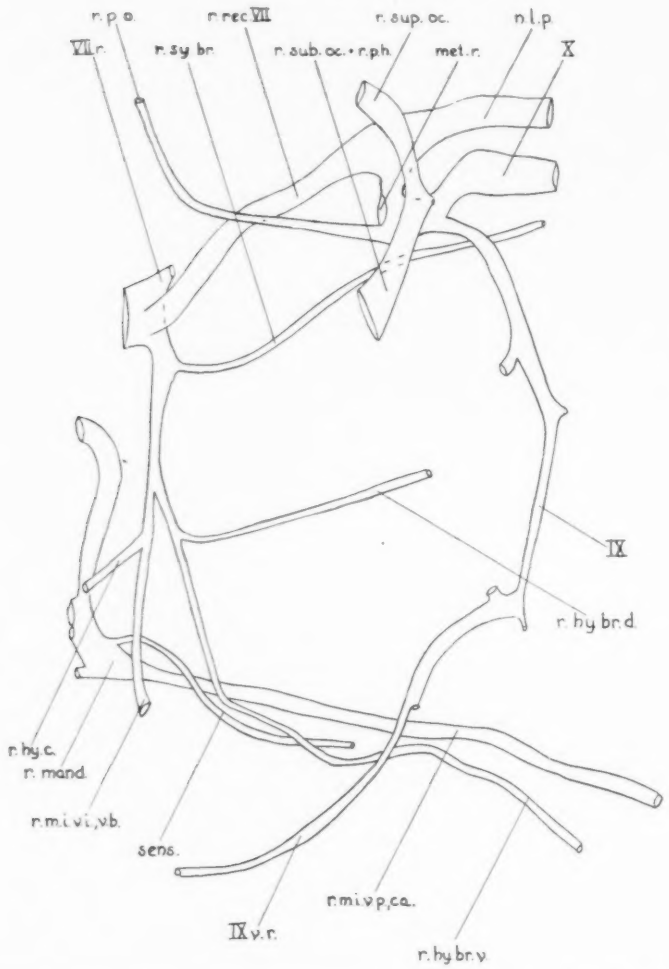

Fig. 34. Petromyzon, adult. Reconstruction of n. facialis and n. glossopharyngeus (incomplete). Lateral view. 25 ×.

thalmicus cannot be entirely excluded, but in the main the buccalis retains its individuality right out to the tip of the snout. R. buccalis innervates also the remaining sense organs in "der Infraorbital-arm". ALLIS's (1934) and HOLMGREN's (1942 b) statement that both "the suborbital and antorbital portions of the line" are buccalis innervated, is thus confirmed. It is, however, difficult to interpret the character of the fibres which run via the commissure from the facial ganglion to the ophthalmic ganglion. If, as TRETJAKOFF states (1927 a), the ophthalmicus innervates the neuromasts dorsal to the eye on the dorsal surface of the head (the pineal line, HOLMGREN), it would be highly

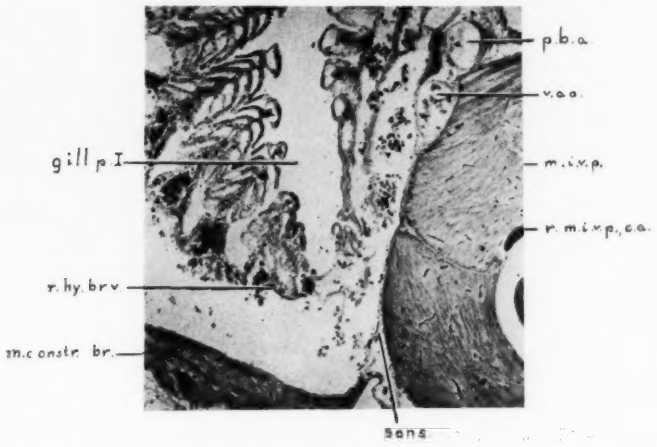

Fig. 35. Petromyzon, adult. Branchial nerve bundles from n. facialis and n. trigeminus (sens.). Transverse section. 55 ×.

probable that the facialis commissure carries lateralis fibres to these neuromasts. TRETJAKOFF is in fact of this opinion. As will be shown later (p. 401), the pineal line is innervated by a branch of the glossopharyngeus, so it is necessary to search for another explanation. Perhaps one cannot entirely rule out the possibility that some neuromasts in "der Infraorbital-arm" are innervated by r. ophthalmicus.

R. recurrens (figs. 29, 34, *r.rec.VII*) runs lateral to the auditory capsule up to the metotic ganglion complex. The nerve certainly gives off fibres between m. supraocularis and m. cornealis to the skin, but not nearly sufficient to supply all the neuromasts in the area (HOLMGREN's, 1942 b, dense row of small neuromasts in the rostral part of the main line). According to HOLMGREN, only the anterior neuromasts are innervated by n. facialis, while the posterior ones in the "dense row" are glossopharyngeus innervated (cf. p. 400 of the present work).

It is unusually difficult to analyse r. sympathico-branchialis (fig. 34, *r.sy.br.*) in detail, and only a summary of a couple of previous studies (JOHNSTON, 1908 a and TRETJAKOFF, 1927 a) will be given here. The nerve runs caudad, ventral to the auditory capsule, and continues along the dorsal walls of the branchial sacs. The nerve runs sometimes medial, sometimes lateral to the origin of mm. constrictores branchiales externus and in the immediate neighbourhood of the anterior cardinal vein. Branches are given off to mm. constrictores where they are lost. So far the descriptions hold for the present material. JOHNSTON considers that r. sympathico-branchialis belongs to the autonomic nervous system and innervates blood vessels in the branchial region.

TRETJAKOFF states that the nerve also carries motor fibres to m. constrictor branchialis externus I.

JOHNSTON (1902, 1908 a) gives a description of r. hyomandibularis (fig. 29, *r.hy.*) which fits in well with the present material. During its course between the styliform cartilage and the extra-hyal, the nerve passes medial to the connecting bridge between these skeletal elements. Here the nerve runs ventro-laterad and sends off motor branches to *m. infravélaire inférieur* etc. (see below), motor branches to m. constrictor branchialis externus I—which lies medial to the nerve—and two retrogressive branchial bundles. One of the last two bundles (fig. 34, *r.hy.br.d.*) runs caudad along the inner side of m. constr. branch. ext. I, approximately on a level with the branchial apertures. Immediately rostral to the sphincter of the first branchial aperture the nerve ramifies into sensory fibres to the mucous membrane of the anterior half of the first gill sac and motor fibres to the sphincter. The other branchial bundle (*r.hy.br.v.*) runs ventro-caudad along the inner side of m. constr. branch. ext. I, crossing the peribranchial venous sinus and running a short distance alongside m. constr. branch. int. (fig. 35). Further caudally the nerve reaches a position close to the lateral side of the pharyngeal roll in a ligament originating in the latter. It retains this position during its subsequent caudal course lying dorso-lateral to the thyroid. So far the nerve has in several places given off thin fibres to the most anterior gill sac. The nerve is lost in the ligament. Its fibres are very fine in calibre and difficult to trace; JOHNSTON (1908 a) is probably right in saying that it innervates gill sacs, blood vessels and the thyroid. JOHNSTON considers it to belong to the autonomic ("sympathetic") system.

The branch of the hyomandibularis which, according to JOHNSTON (l.c.), innervates *m. infravélaire inférieur* (hyo-hyoideus anterior in his terminology), is found in the present material (fig. 34, *r.m.i.v.i., v.b.*). The nerve runs ventro-mediad from r. hyomandibularis to the pharyngeal roll. Here, in addition to the muscle already mentioned, it innervates *m. vélaribranchial*, which was hitherto considered to belong to the trigeminal musculature.

The main trunk of r. hyomandibularis (fig. 29, *r.hy.c.*) makes its way to the subcutis ventral to n. subocularis and dorsal to r. posthyoideus, and in doing so pierces the posterior part of m. subocularis. Most of the nerve branches run rostrad and supply—as JOHNSTON states—the skin on the ventro-lateral side of the head and neuromasts. The neuromasts are partly those lying in the accessory branch of "der Inframaxillar-arm" (MERKEL, 1880) and partly the most anterior ones in "der Inframaxillar-arm" (the oral line and the longitudinal line branching off from it, HOLMGREN, 1942 b). The question as to whether the most anterior neuromasts in the accessory branch are innervated by the trigeminus or the facialis is discussed on page 382. If all the neuromasts belong to the hyomandibularis innervation region, it is

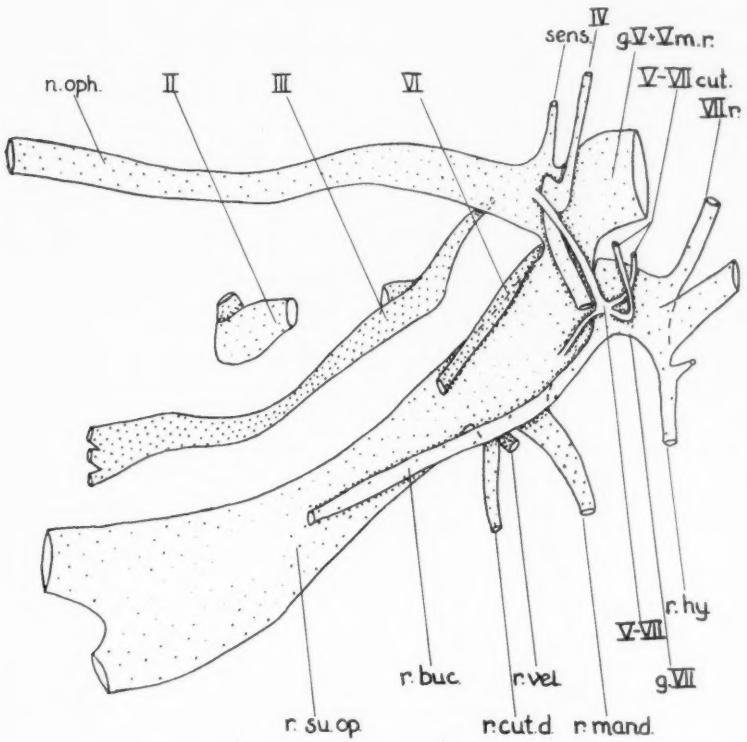

Fig 36. Petromyzon, adult. Reconstruction of the eye muscle nerves and some trigeminal and facial nerves. Lateral view. 33 ×.

difficult to understand the character of the commissure between the facialis and the V_2-ganglion. The situation is thus parallel to that discussed on page 388 regarding the lateralis component of the ophthalmicus.

In addition to the branches of the hyomandibularis described by previous writers, a thin bundle of fibres is given off by the nerve when it reaches a point immediately adjacent to the medial surface of m. subocularis, rostral to the extra-hyal (fig. 29, *com.*). In aberrant specimens it is difficult to follow the thin bundle. It runs caudad, lateral to the extra-hyal, piercing m. subocularis, and gets in contact with r. cutaneus descendens. Its character is discussed on page 379.

3. THE NERVES OF THE EYE MUSCLES.

Unless otherwise stated, the descriptions refer to adult P. planeri and fluviatilis. P. FÜRBRINGER's (1875) names for the eye muscles are used.

A. N. Oculomotorius.

The nerve (fig. 36, *III*) runs between n. ophthalmicus and r. subopticus and innervates m. rectus superior and anterior and m. obliquus anterior. It passes ventral to n. opticus. For the innervation of m. rectus inferior, see below. KOLTZOFF (1902) and DAMAS (1944) describe no primordium of a ganglion ciliare in the Petromyzon embryo. TRETJAKOFF (1909 b) mentions a n. mesencephalicus in Ammocoetes connecting the mesencephalon with the ophthalmic ganglion. The same writer (1926 a, 1927 a) describes "sympathetic" cell bodies in the peripheral course of the oculomotorius and in the connective tissue sheath of n. opticus. These two groups of cell bodies may, according to TRETJAKOFF, correpond to the ciliary ganglion in Gnathostomes. He also describes (1927 a) some nn. ciliares which are said to run from the V_2-ganglion via m. rectus inferior to the ciliary body and the iris. This area is possibly also innervated by branches from n. ophthalmicus. Nn. ciliares are said to be exclusively sensory. Petromyzon lacks intrinsic eye muscles according to the same author. It has not been possible to find any nn. ciliares in the present material, nor any peripheral cell bodies. It is, however, not out of the question that cell bodies would be observed if another method were used. Only a comment on TRETJAKOFF's work will therefore be made. The ciliary complex in Gnathostomes includes parts of the ophthalmicus and the oculomotorius and forms a connection between these nerves, which is difficult to analyse in detail (HALLER, 1934). It is, therefore, noteworthy that there is no contact between n. oculomotorius and n. ophthalmicus in Petromyzon.

B. N. Trochlearis.

The present material confirms the generally accepted opinion that n. trochlearis in Petromyzon (fig. 36, *IV*) runs dorsal to n. ophthalmicus. According to TRETJAKOFF (1927 a), KOLTZOFF (1902) is of another opinion, and, moreover, he states that KOLTZOFF has confused n. trochlearis and "n. cornealis". TRETJAKOFF seems, however, to have misunderstood KOLTZOFF. The intersection of the trochlearis and the ophthalmicus lies proximal to the V_1-ganglion. The possibility of an exchange of single fibres between the nerves cannot be ruled out. During its subsequent peripheral course the trochlearis runs ventrad, lateral to the ophthalmicus, passing an area limited medially by the trigeminal and the facial ganglia and laterally by the commissures between the facial and ophthalmic ganglia. A certain amount of variation occurs, however. In some specimens fibres of the commissure between the facial ganglion and the ophthalmic ganglion pierce the trochlearis, in others the entire trochlearis runs lateral to the commissure. It is remarkable that the trochlearis is able, in this way, either to run through or to skirt entirely an area which is so well defined by other nervous elements.

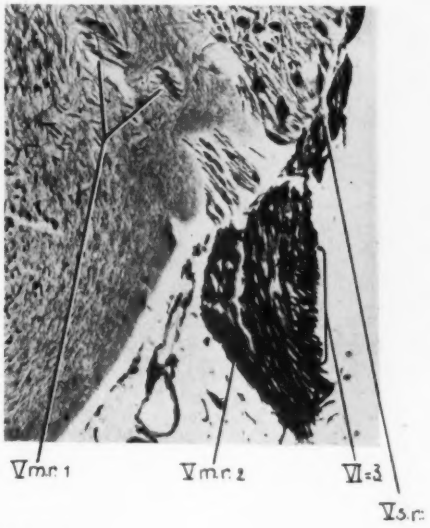

Fig. 37. Petromyzon, adult. Two small rostral motor root bundles of the trigeminus in the brain (*1*), the main motor trigeminal root (*2*) and the abducens (*3*). Transverse section. 135 ×.

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C. N. Abducens.

P. FÜRBRINGER describes (1875) how m. rectus inferior in Petromyzon is innervated from the abducens instead of from the oculomotorius as in Gnathostomes. Since then several writers have tried to find an explanation of this condition in lack of homology between certain of the eye muscles in Cyclostomes and Gnathostomes or in displacement of the muscles. CORDS (1929 a) treats the literature on the subject. Other writers have made new studies of the nerves themselves and discussed their findings. The work of these writers will be dealt with in some detail here. AHLBORN (1884 a and b) describes three root bundles in the motor complex of trigeminus-abducens (cf. 1884 a, figs 20 and 21 and figs. 37, 39 in the present work). A small bundle emerging rostrally (fig. 37, *V.m.r.1*) is called abducens by AHLBORN. In a cross-section of the medulla, it runs dorso-medial to the largest bundle in the complex. It originates in a rostral part of the motor nuclear region of the trigeminus. The largest bundle in the complex (figs. 37, 39, *V.m.r.2*)—called by AHLBORN the transverse trigeminal root—originates in the main part of the motor nuclear region of the trigeminus. Caudal to this root emerges the third root—a small bundle (fig. 37, *VI=3*, fig. 39, *VIr*). This is called by AHLBORN the descending trigeminal root. It runs caudad in the medulla and its nucleus is unknown to AHLBORN. In later descriptions these three bundles have various names. They will be referred to as roots 1, 2 and 3 in the following survey of the literature. As the position of the nucleus of abducens is not absolutely fixed, and as the innervation of m. rectus inferior has not yet been explained, there is good reason to consider in detail the extensive literature on the subject.

A) SCHILLING (1909) and SAITO (1930) could not identify the root and nucleus of the abducens.

B) Some writers consider roots 2 + 3 to contain both motor and sensory trigeminal fibres and abducens fibres. (TRETJAKOFF, 1909 a, 1927 a, and ADDENS, 1933.) TRETJAKOFF calls this complex the "untere gemischte" trigeminal root, implying that No. 3 contains the sensory component.

C) ADDENS has given a new interpretation of root 1. ADDENS (1933) describes two small root bundles emerging rostrally and puts forward the hypothesis that they are caudal oculomotor roots. Their course would thus differ from that of the rest of the oculomotorius. After emerging from the medulla they would join the abducens (see under B). If this be the case, then the innervation of m. rectus inferior is explained. (CORNING, 1902, inclined to the view that an intracranial connection exists between the oculomotorius and the abducens.) TRETJAKOFF (1930) considers that ADDENS's explanation is probably correct. STEFANELLI (1935) agrees with ADDENS regarding root 1. HEIER (1948, p. 179) says—when speaking of these caudal oculomotor roots—"whether the two rhombencephalic nuclei represent nuclei of eye muscles was however not confirmed". ADDENS describes *two* small caudal oculomotor roots where other writers describe one rostral trigeminal motor root. ADDENS states, however, and the present material confirms that it is doubtful whether there are one or two bundles. Outside the brain one can certainly see two distinct bundles, but inside the brain they run in certain specimens as one bundle, in others as two.

When judging ADDENS's hypothesis one should bear in mind that he did not follow the abducens either peripherad or centrad.

D) The following authors have in the opinion of the present writer interpreted the root of the abducens correctly. JOHNSTON (1902) doubts the accuracy of AHLBORN's statement that root No. 1 belongs to the abducens. Such a statement implies that the abducens comes from the visceral motor nuclear column. JOHNSTON puts forward an alternative hypothesis that the abducens may prove to be identical with the fibres in the motor complex of the trigeminus "which arise from the ventral column in the region of VII and VIII", i.e. root 3.

It is probable that STEFANELLI (1935) belongs to this group. He describes root 3 in P. marinus as a possible abducens root, but describes in addition a root with a somewhat different course which could be followed caudad to the somatic motor column at the level of the facialis nucleus. He considered that this somatic motor root belongs quite definitely to the abducens. If this is so, then the course of the abducens in P. marinus differs from that in P. planeri and fluviatilis in some respects.

WOODBURNE (1936) points out that root 1 does not join the abducens when it emerges from the brain, but can be traced to the musculature "in the floor of the oral cavity". According to WOODBURNE, root No. 1 originates in the nuclear region of the motor trigeminus. He also states that the remainder of

Fig. 38. Petromyzon, adult. Position of n. abducens in an aberrant specimen. The nerve has passed between the motor and the sensory trigeminus and will run straight to the orbit (left). Transverse section. 95 ×.

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the motor root complex of the trigeminus consists of both a large, exclusively motor root (No. 2) and a descending root (No. 3). This descending root contains both trigeminal motor fibres and a bundle whose destination he is not able to fix. According to JOHNSTON's alternative hypothesis (see above), this bundle is the abducens which has its nucleus in the ventral motor column "at the level of the acustico-facialis gray". WOODBURNE considers that JOHNSTON's explanation "most clearly corresponds to the indications in the material studied".

It should be pointed out that no one has hitherto been able to trace the abducens from the periphery through the root complex to any of the root bundles 1, 2 or 3. STEFANELLI (1935), who gives possibly the most concrete description of the central nucleus of the abducens (see the reservation above) cannot have traced the nerve coming from the root in a peripheral direction as he accepts ADDENS's interpretation of "the posterior oculomotor roots".

E) TRETJAKOFF (1926 a, 1927 a) states that m. rectus inferior is innervated partly by the abducens but also partly by a thin branch of n. oculomotorius. CORDS denies this (1929 a, b), but TRETJAKOFF adheres to his statement (1930).

The present observations concern the peripheral course of the nerves and the course of the roots up to and including their most distal course in the medulla, but not the connections of the nerves to their nuclear regions. The present author is able to confirm AHLBORN's anatomical description, given above, but cannot, on the other hand, agree with his interpretation. WOODBURNE's statement that root 1 does not join the abducens but runs out into the trigeminal musculature is confirmed in the present material. Root No. 3 belongs to the abducens—with the possible exception of a few motor fibres

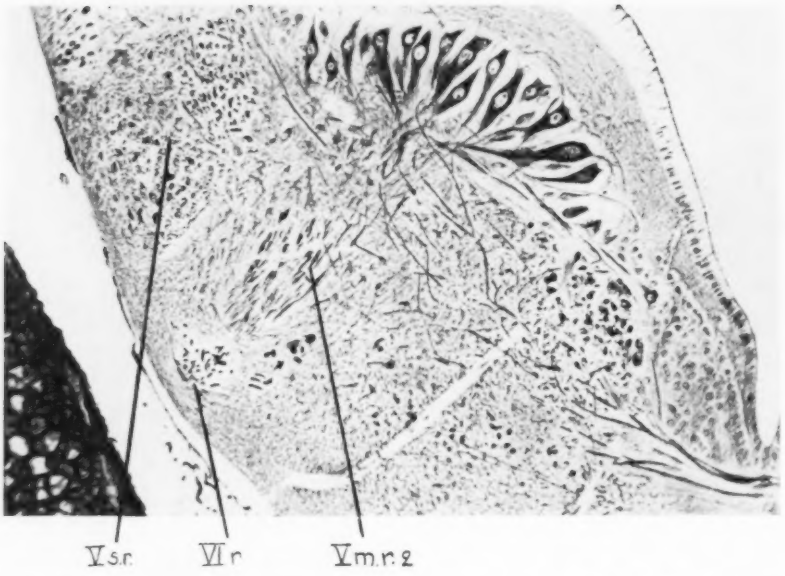

Fig. 39. Petromyzon, adult. Transverse section through the medulla. The main motor trigeminal root and the abducens root. The section lies caudal to that in fig 37. 125 ×.

of the trigeminus; see WOODBURNE under point D. The abducens can be traced from its course in the medulla through the root complex to the periphery.

After leaving the brain immediately caudal to the large motor root of the trigeminus, the abducens (figs. 36, 37, 39, 40) runs lateral to the motor V, and—further peripherally—between the latter and the sensory root of the trigeminus. From about this point and more peripherally, AHLBORN's (1884 a) and TRETJAKOFF's (1930) descriptions are confirmed. The abducens passes the root of the V_2-ganglion on the medial side and finally reaches a position dorsal to the V_2-ganglion and ventral to the ophthalmicus. From here it runs laterad out into the orbit and innervates m. rectus posterior and inferior. The possibility of an exchange of single fibres between the trigeminus and the abducens cannot be entirely ruled out in any of the specimens in the present material. A surprisingly great departure from the above course is observed in two specimens of P. planeri, though only on one side in both specimens. From its position between the motor trigeminal root and the sensory V-root, instead of running medial and dorsal to the V_2-root, the abducens runs laterad, ventral to the V_2-root, out into the orbit and makes its way to the musculature (fig. 38. Cf. fig. 23). Such a marked difference in the relations between the trigeminus and the abducens is the strongest expression the present writer has found of the variations of which the nervous system in Petromyzon seems capable.

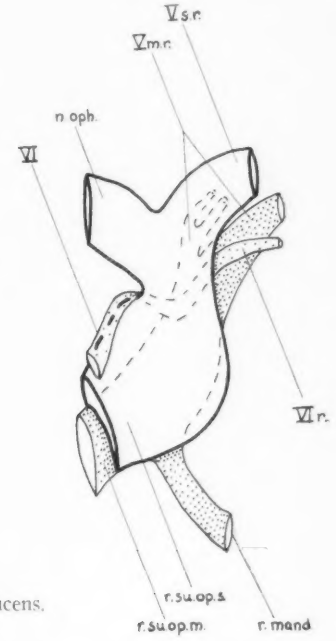

Fig. 40. Petromyzon, adult. Reconstruction of n. abducens. Lateral view. 33 ×.

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Study of a P. fluviatilis specimen in the present material confirms TRETJAKOFF's statement (1926 a, 1927 a, 1930) that m. rectus inferior is innervated, apart from n. abducens, by a thin branch of n. oculomotorius, but the oculomotor innervation was not observed in any of the P. planeri specimens studied. It appears as if ontogenetic studies are the only possible way of solving the problem of the innervation of m. rectus inferior. DAMAS (1944), who should have had good opportunities for solving the problem, states, however, that Petromyzon is particularly unsuitable for such studies owing to the embryonic character of the eye muscles during the long larval period.

It is not the intention of the present author to under-value the accurate analyses of n. abducens carried out by JOHNSTON (1902) and WOODBURNE (1936), but the present investigation should increase the factual background for the following discussion. Since the root of the abducens has, in all probability, its nucleus in the ventral motor column at the level of the acusticofacialis gray (as stated by JOHNSTON, STEFANELLI and WOODBURNE), the abducens' character as a somatic motor nerve is established. Considering that the nucleus lies so far caudally it is reasonable to assign the facialis and the abducens to the same neural segment. This is of course also evident from KOLTZOFF's (1902) and DAMAS' (1944) embryologic studies of the segmentation of the head. It should be pointed out that the motor nucleus of the facialis occupies an exceptionally rostral position in the Cyclostomes, which is

considered to be primitive (ARIENS KAPPERS, 1910, 1912, RÖTHIG, 1914, BLACK, 1917, v. DER HORST, 1918, ADDENS, 1933, ARIENS KAPPERS *et alii*, 1936).

All three eye muscle nerves are found in Ammocoetes. N. trochlearis runs close against the ophthalmic ganglion as in the adult, but the nerve also runs alongside the dorso-lateral surface of the V_2-ganglion, and here too an exchange of fibres may take place. In the specimens of Ammocoetes studied, the trochlearis runs through the area bounded by the trigeminal and the facial ganglia and the commissure between them. The abducens could not be traced mediad further than to a point between the two trigeminal ganglia.

4. THE METOTIC CRANIAL NERVES.

In the present material this nerve group has only been studied in P. planeri.

During the last century great interest was paid to the number and arrangement of the roots of the vagus group in Petromyzon, the problem being to find a serial homology between the most posterior nerves of the brain and the spinal nerves. SCHNEIDER (1879), for example, considered that there was a similarity between the pairs of spinal nerves formed by dorsal sensory and ventral motor roots and the vagus-"hypoglossus" pair, in which the vagus was considered exclusively sensory and the "hypoglossus" (i.e. the most anterior spinal nerves, see below) exclusively motor. Studies of the ontogenesis and of the central nervous system and studies of the sensory endings of the nerves in Vertebrates led, towards the end of the 19th century, to the formulation in its modern form of the principle of the functional components of the nervous system. This involved a revaluation of n. vagus as a segmental nerve. The interpretation of the most anterior of the spinal nerves in Petromyzon as a "hypoglossus" was abandoned, since NEAL (1897) pointed out that the further caudally lying connection between the spinal nerves and n. vagus is a true n. hypoglossus (cf. also v. KUPFFER, 1893—1900, part 3 and M. FÜRBRINGER, 1897, page 604). This connection was discovered by BORN (1827), but its true *character* as a n. hypoglossus is established by NEAL's and FÜRBRINGER's works. FÜRBRINGER, however, does not accept the *name* "hypoglossus" for the nerve in Petromyzon. (If a detailed resemblance between the nerve in Petromyzon and n. hypoglossus in higher Vertebrates is demanded to justify the use of the name "hypoglossus" for the nerve in Petromyzon, then the name certainly should be abolished in descriptions of Petromyzon.) JOHNSTON (1902, 1905, 1908 a) carried out an analysis of the cranial and spinal nerves in Petromyzon based on the concept of the functional divisions of the nervous system. A modern account of the morphogenesis of the metotic region may be found in DAMAS (1944).

A large number of descriptions have been published of the mutual connec-

tions between the metotic nerves and their connections to r. recurrens VII. (Cf. in the recent literature: AHLBORN, 1884 a and b, JULIN, 1887, ALCOCK, 1899, JOHNSTON, l.c., SCHILLING, 1909, TRETJAKOFF, 1927 a and CORDS, 1929 a) A description will also be given here—it contains nothing that has not in one way or other been put forward already. It is easier to trace the roots between the ganglia and the medulla in Ammocoetes than in the adult. In the adult the roots were only sufficiently delimited in one favourable specimen. The following description should hold true for both Ammocoetes and the adult animal. The glossopharyngeus and the lateralis posterior originate from the rostral roots in the metotic complex, and from this glossopharyngeus-lateralis group a branch is sent off which joins the roots of the vagus, which are otherwise more caudal in origin. Further distally the glossopharyngeus separates from the lateralis posterior. The latter approaches the vagus instead. The ganglion of the glossopharyngeus is well separated from the other ganglia, whereas the vagus ganglion and the lateralis ganglion (ganglion metoticum) lie close to each other, fibres running between them. When r. recurrens VII approaches the metotic ganglion, it lies in intimate contact with r. supraocularis. R. recurrens sends its fibres chiefly into the ganglion of the lateralis posterior. A number of fibres, which do not run out with n. lateralis posterior, are lost in the ganglion or can be traced down to the vagus ganglion.

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According to JOHNSTON, the glossopharyngeus, the vagus, and the lateralis posterior are clearly separated from the point where their roots emerge from the medulla, apart from one nerve bundle which runs in Ammocoetes of P. dorsatus from the lateralis posterior to the vagus (proximal to the ganglia). In the same species r. recurrens VII is said to send its fibres both into the lateralis posterior and into the glossopharyngeus, carrying lateralis fibres to these nerves. He also states that in adult Lampetra Wilderi the lateralis posterior gives off, instead, a branch to n. glossopharyngeus, and that in this species r. recurrens VII unites with the lateralis posterior and the vagus. According to JOHNSTON, the glossopharyngeus and the vagus carry general cutaneous, visceral sensory and visceral motor fibres from the medulla.

DOHRN (1888) is the only writer to have said anything about the direction in which r. recurrens VII develops during the ontogenesis. He states that the nerve develops in a caudal direction. He also states that n. lateralis posterior is developed before r. recurrens reaches the metotic region. From this one may conclude that the fibres in r. recurrens have their cell bodies in the facial ganglion. This, of course, agrees well with the fact that most of the recurrens fibres accompany n. lateralis posterior peripherad. The rest may in the present material either join the vagus and make their way to the neuromasts of the latter or return to the brain. It seems unlikely that n. glossopharyngeus receives a contribution from r. recurrens. This agrees with JOHNSTON's statement of the conditions in Lampetra Wilderi. There appears

to exist a considerable difference between the lateralis system in this animal and in Ammocoetes of P. dorsatus (JOHNSTON, 1905), since in the latter r. recurrens is said to carry *inter alia* prootic lateralis fibres to n. glossopharyngeus and its neuromasts. If one assumes that the recurrens fibres which do not accompany the lateralis posterior re-enter the medulla, the difference is not so great; JOHNSTON does not, however, appear to consider such a solution probable. There is another possible solution. The connection between r. recurrens VII and n. glossopharyngeus—which JOHNSTON (1905) shows in fig. 11—is perhaps r. postorbitalis IX, which JOHNSTON does not describe in this species (cf. fig. 41). The question still remains as to how n. glossopharyngeus receives its lateralis component in P. dorsatus, a question that can only be answered by renewed studies of the medulla. It seems most probable that n. glossopharyngeus in P. planeri receives its lateralis component exclusively from the lateralis posterior, whereas the vagus receives its lateralis component from the lateralis posterior and possible from r. recurrens.

N. Glossopharyngeus.

Only two of the peripheral branches of the glossopharyngeus will be described in detail. SCHLEMM-D'ALTON (1838) mention that the first branchial nerve is a combination of a root from the glossopharyngeus-vagus complex and a branch of the "hypoglossus". The connection between n. glossopharyngeus and the "hypoglossus" is, however, r. postorbitalis. ALCOCK (1899, p. 144) makes the next contribution to the knowledge of r. postorbitalis in as much as she describes a dorsal branch of the glossopharyngeus which "passes outward to the external side of the auditory capsule, where it runs forward between the dorsal and ventral portions of the first myotomes, close to the ramus recurrens facialis, with which it might easily be confused. It passes to the skin and supplies the epithelial pits forming the posterior part of the row on the dorsal surface of the head, continuous with those supplied by the ramus ophthalmicus superficialis". (The name r. ophthalmicus superficialis was altered by COLE, 1899, to r. buccalis.) In the present adult material, the nerve (fig. 41, fig. 34, *r.p.o*) passes immediately dorsal to the common trunk of r. posthyoideus and r. suboccularis, so close to the trunk that it is impossible to say wether or not it picks up fibres from the trunk. Probably it does, because the ribbon-shaped and somewhat sparsely fibred nerve bundle, which comprises r. postorbitalis lateral to the auditory capsule, innervates the spinal part of m. cornealis (p. 418) TRETJAKOFF (1927 a) states that this muscle is innervated by the trigeminus, whereas CORDS (1929 a), who does not describe a r. postorbitalis, says that m. cornealis is innervated from the spinal nerves. Lateral to the auditory capsule, the postorbitalis passes lateral to r. recurrens facialis. In the adult, the nerve can be traced further peripherally than the point described by ALCOCK as the

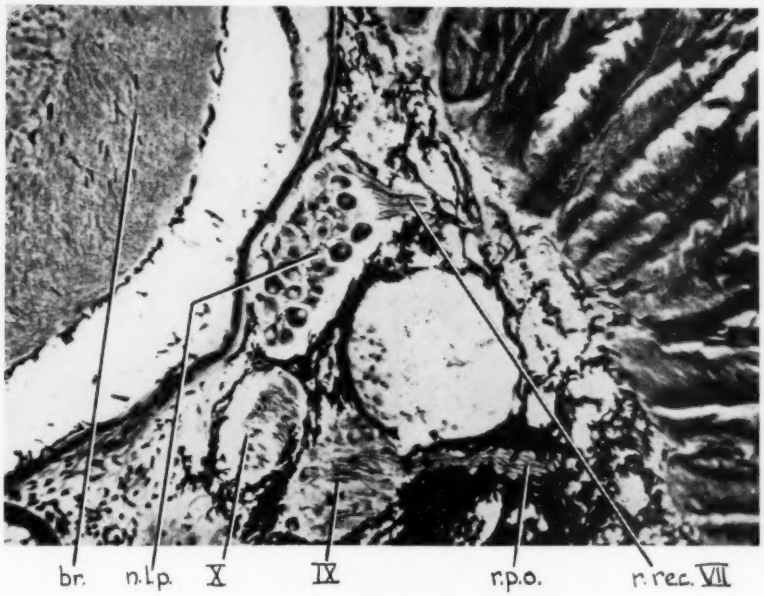

Fig. 41. Ammocoetes. The origin of r. postorbitalis. Transverse section. 180 ×.

end. The nerve leaves the myoseptum between m. supraocularis and m. cornealis and ascends dorsad and rostrad, running in the subcutis. The final terminal branches innervate the neuromasts dorsal to the eye, which MERKEL (1880) calls "der Verbindungs-arm" i.e. the pineal line according to HOLMGREN (1942 b). These neuromasts are, according to TRETJAKOFF (1927 a), ALLIS (1934) and HOLMGREN, innervated from the trigeminus.

The branch of the glossopharyngeus dorsal to the auditory capsule, described by HATSCHEK (1892) and JOHNSTON (1902), could not be found in the present material.

ALCOCK describes (1899) a branch of the glossopharyngeus to the neuromasts lying on the ventral side in Ammocoetes (corresponding to MERKEL's "Inframaxillar-arm" in the adult, that is the line which HOLMGREN describes as a longitudinal line branching off from the oral line). A similar nerve branch is found in adult P. planeri and fluviatilis in the present material (figs. 29, 34, *IXv.r.*). The branch is one of those skin branches given off ventrally from the trunk of the glossopharyngeus (cf. TRETJAKOFF, 1927 a, p. 408). It passes rostral to the first branchial arch and proceeds rostrad in the subcutis and passes ventral to the skin branches from r. cutaneus descendens and from r. hyomandibularis. Most distally it runs almost ventro-medially in the body. It has been followed to a transverse plane lying somewhat rostral to the eyes. It innervates both the neuromasts in "der Inframaxillar-arm" and the skin on the ventral side.

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5. THE SPINAL NERVES.

The most anterior spinal nerves have been studied in adult P. planeri in the present material. TRETJAKOFF (1927 a) uses the term spino-occipital for these nerves. Since branches of the further caudal spinal nerves probably represent a n. hypoglossus, it might be better to use a more neutral name. There is moreover a certain lack of agreement between text and figures in TRETJAKOFF's description of the spino-occipital nerves. In the text (pp. 410—413) no description is given of a root and ganglion of a second dorsal sensory nerve. Such elements are, however, depicted in fig. 21 and are clearly identical with those given in the text as the root and ganglion of the third dorsal sensory nerve. TRETJAKOFF probably altered his opinion as to which dorsal and ventral roots belong together in pair. In the present material are found the nerves (roots) which TRETJAKOFF calls in the *text* (pp. 410—413) first, second and third ventral and first and third dorsal. These names for the nerves will be used hereafter. There is little to add to his description. The common trunk from the first and second ventral root (fig. 34, *r.sub.oc.* + *r.p.h.*) probably innervates part of m. cornealis (p. 400). The third dorsal root appears to send off rostrad a few fibres alongside r. supraocularis. The third ventral root, also, has a few bundles running rostrad alongside r. supraocularis. The relations between the third dorsal and the third ventral root and the first spinal arch vary. The more rostrally emerging spinal nerves all pass rostral to the first spinal arch. In TRETJAKOFF's table, page 428, n. occipitalis II is given as supplying m. supra- and subocularis and the skin outside these muscles. This statement, which implies that the nerve in question innervates a widespread area of the skin, has no parallel in the text, and is probably a lapsus.

N. hypoglossus and the morphogenetical questions connected with it have not been studied on the present material, but as this region has been touched on in a couple of discussions already, a short resumé of some works which deal with the nerve and the problem in question will be given here. KOLTZOFF (1902) and DAMAS (1944) state that even the most anterior metotic myotomes are developed in Petromyzon. From here come *inter alia* m. supra- and subocularis, m. praebranchialis and m. cornealis. These muscles cover a considerable part of the head rostral to the branchial region. M. subocularis does not develop before the metamorphosis and belongs to *les myomères hypotrématiques* (DAMAS, cf. also p. 418). The three most anterior spinal nerves differ from those that follow; the first and second ventral nerves extend widely in the above-mentioned musculature. Posterior to the three most anterior nerves follow a number of spinal nerves which send off branches to the vagus. These branches accompany the vagus caudad, and then, caudal to the gill basket, they bend rostrad as an independent n. hypoglossus and innervate *les myomères*

hypotrématiques (except m. subocularis). Cf. NEAL (1897), JOHNSTON (1905) and DAMAS (1935, 1944). In Gnathostomes two myotomes are more or less completely reduced immediately behind the auditory capsule. The reduction (during the development from the Cyclostome stage to the Gnathostome stage) of m. supra and subocularis and the nerves belonging to them results in one of the most striking differences between the anatomy of the head in Cyclostomes and Gnathostomes.

6. AMMOCOETES AND THE ADULT PETROMYZON.

There is a certain risk in identifying structures in Ammocoetes with those in the adult, a risk which should be obvious ever since SCHNEIDER (1879) showed that the larval muscles in the trigeminal region are partially or completely broken down before the adult muscles are formed. The great changes taking place during the metamorphosis must naturally be reflected in the nervous system. A number of nerve fibres should, for example, develop to the newly-built muscles. A count of the number of motor fibres in some trigeminal branches in Ammocoetes and in the adult is sufficient evidence of this. JOHNSTON (1902, 1905, 1908 a, 1910), STEFANELLI (1937) and LARSELL (1947 a) analysed the brain in both the adult and Ammocoetes. They showed that the brain is a complex structure exhibiting considerable similarities in the two stages. It is in fact the complex structure of the brain that justifies comparisons being made even in the absence of studies of metamorphic material. On the basis of the above works it is possible to define the nerves emerging from the brain by means of their central connections and the character of their peripheral terminations. It remains to discover whether the nerves in the adult and in Ammocoetes have similar ramification patterns and similar courses relative to the structures whose transformation during the metamorphosis is known.

A. N. Trigeminus.

KAENSCHE (1890), BUJOR (1891, 1892) and DAMAS (1935) studied the development of the buccal cavity and the suctorial disc during the metamophosis. DAMAS states that "La ventouse de la Lamproie correspond uniquement à la région papillaire du vestibule buccal de l'Ammocoete". He also points out the correspondence between the tentacles in the larva and the cornual teeth in the suctorial disc of the adult. The three writers just mentioned and JOHNELS (1948) describe how the medial tentacle and its caudal elongation in Ammocoetes are transformed into the piston mechanism of the adult. BALABAI (1946) states that a direct sequence in the praebranchial region during the metamorphosis can be observed only in the upper lip and the area where the medial tentacle and the piston mechanism lie.

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In Ammocoetes and in the adult the dorsal wall of the buccal cavity is innervated by r. suprapharyngeus which originates at a proximal point on r. subopticus. Distal to this point, the main trunk of r. subopticus divides into three branches: r. apicalis, r. basilaris and r. suborbitalis. In Ammocoetes "r. apicalis" gives off r. subpharyngeus at the same place, but in the adult this branch is not given off by r. apicalis until a point further rostral. This is probably due to the extension of the rostral part of the head during the metamorphosis, described by, for example, DAMAS (1935). (The reason for the citation of "r. apicalis" in Ammocoetes is given on p. 405.) R. subpharyngeus may possibly innervate some ventro-lateral tentacles and cornual teeth, respectively, but innervates chiefly the medial tentacle and the rostral head of the piston mechanism, respectively. In the adult it also innervates some muscles in this head. R. subpharyngeus gives off a branch—r. recurrens—caudad. R. recurrens runs along the ventral wall of the buccal cavity, dorsal to the rostrally directed motor branches of r. mandibularis. In Ammocoetes the nerve lies laterally in the fold which is the caudal elongation of the medial tentacle. JOHNELS (1948) describes the development of this medial fold up to a late stage in the metamorphosis. It is of some interest that r. recurrens in the adult lies during its most caudal course in a very slight fold in the medial wall of the buccal cavity. After it has given off r. subpharyngeus, r. apicalis (r. perforans in the adult) innervates a number of muscles and, in addition, the oral hood and the suctorial disc, respectively, supplying *inter alia* tentacles in the oral hood and the cornual teeth in the suctorial disc, except for the tentacles and the cornual teeth innervated by r. subpharyngeus. The fibres constituting r. suborbitalis and r. cutaneus descendens emerge from the lateral part of the V_2-ganglion. The nerves are both exclusively cutaneous. R. suborbitalis is at first part of r. subopticus and is only further distally an independent nerve. In some specimens of Ammocoetes and of adult Petromyzon, r. cutaneus descendens emerges as two branches which unite. The peripheral distribution region of r. cutaneus descendens lies both in Ammocoetes and in the adult rostral and rostro-ventral to the first external branchial aperture, and in both stages the nerve unites with a branch of the hyomandibularis. DAMAS (1935) discovered that m. subocularis develops from a primordium which remains in an embryonic state throughout the entire larval period. Thanks to this discovery, it is possible to compare the relations between r. suborbitalis, r. cutaneus descendens, r. hyomandibularis and the spinal musculature in Ammocoetes and in the adult (p. 418).

It is difficult to compare the motor elements in r. subopticus in Ammocoetes and in the adult. In the adult, r. basilaris is divided into a medial and a lateral branch. The medial branch runs alongside r. apicalis and the lateral alongside r. suborbitalis. In Ammocoetes there is a motor main trunk which runs ventrad from the ramification point of r. subopticus. This motor nerve may

be called preliminarily "r. basilaris". The nerve has, it is true, both medial and lateral branches, but "r. apicalis" in Ammocoetes may very well contain a branch corresponding to the medial branch of r. basilaris in the adult. It is difficult to come to a decision as both "r. apicalis" in Ammocoetes and r. apicalis in the adult contain a motor component. The problem can only be solved by studying the metamorphosis. JOHNELS (1948, p. 193) describes a phase in the transformation of r. basilaris during the metamorphosis, but when he states that "scattered fibres ... begin to collect into a nerve" he does not appear to have taken into consideration the fact that the adult r. basilaris is already divided into two well-separated branches at its origin in r. subopticus. In Ammocoetes the motor branches of r. subopticus innervate their muscles within a rather limited area. In the adult, the medial basilaris branch ramifies at a point considerably rostral to the region in which the lateral branch splits up. This difference is certainly due to the extension of the rostral part of the head during the metamorphosis.

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HOLMGREN—STENSIÖ (1936) compare the lateral mouth plate in Ammocoetes to the anterior lateral plate in the adult, and HOLMGREN (1946) interprets the anterior lateral plate as an internal praemandibular arch. JOHNELS (1948) has shown that the anterior lateral plate develops during the metamorphosis medial to the lateral mouth plate, and that a ventral branch of "r. maxillaris" runs down between the skeletal elements in the stages of the metamorphosis where both skeletal elements could be identified. Judging from JOHNELS's description (pp. 197—198), the nerve branch is probably r. subpharyngeus. When JOHNELS (p. 255) says of the lateral mouth plates: "Since certain parts of the suborbital nerve (V) run on their inner side, they may represent an extra-premandibular", he is probably referring to r. subpharyngeus. JOHNELS's statement must refer in the first place to certain stages in the metamorphosis. In Ammocoetes the nerve lies in a more medial position than the lateral mouth plate, but only a few small branches actually run medial to the skeletal plate (fig. 27, *sens.*). Another branch of r. apicalis passes medial to the lateral mouth plate (fig. 27, *r.ap.II*). The rest of r. apicalis—like the other trigeminal branches—runs lateral to the lateral mouth plate. It would seem that the course of r. subpharyngeus and one other branch of r. apicalis medial to the lateral mouth plate is in itself insufficient grounds for the hypothesis that this skeletal element is an external arch.

Both HOLMGREN and JOHNELS interpret the anterior lateral plate of the adult as an internal arch. The course of r. subpharyngeus and r. perforans, lateral to the primordium of this skeletal element during the metamorphosis, supports such an interpretation (JOHNELS). In the adult the terminal branches of r. subpharyngeus lie in the head of the piston mechanism, medial to the anterior lateral plate, and r. perforans runs laterad, ventral to the skeletal plate. A change in the relations between the anterior lateral plate and the branches of

r. apicalis must presumably take place during the later stages of the metamorphosis; there is need for an investigation into the details of this change.

Of the remaining trigeminal branches, we shall discuss r. velaris and r. mandibularis. (A number of small motor and sensory branches which emerge in the adult from the point where the V_2-complex splits into r. subopticus and r. mandibularis will not be dealt with here.) The velum and its transformation during the metamorphosis have been studied by DAMAS (1935), who also gives an account of the earlier literature on the subject. According to DAMAS, the only muscle bundles which can be identified in Ammocoetes, in the various stages of the metamorphosis and in the adult lie in the velum. The velum and the corresponding structure in the adult are richly innervated by sensory trigeminal branches. The mucous membrane facing the buccal cavity is particularly well supplied. No r. velaris in the form of a genuine branch can be found in the larva—at least not in all specimens—whereas r. velaris in the adult contains most of the sensory fibres in question. R. mandibularis, however, also contains a number of sensory fibres to the velum and to the corresponding structure in the adult. The motor branches in r. mandibularis in Ammocoetes and in the adult are difficult to compare; this is not surprising since there is only a thin layer of musculature ventral to the buccal cavity and the pharynx in Ammocoetes and the musculature of the piston mechanism only develops during the metamorphosis. Even if the trunk of the mandibularis running rostrad in Ammocoetes can be considered to correspond to the branches which in the adult run rostrad up to *m. velari-apical*, m. anuloglossus, etc., the larva nevertheless definitely lacks any homologue to the branches which run caudad in the adult to *m. infravélaire postérieur*, m. cardio-apicalis, etc.

B. N. Facialis.

NESTLER (1890), WEISSENBERG (1926) and KEIBEL (1927) studied the metamorphosis of the branchial part of the gut. The changes in the facialis musculature during the metamorphosis are not extensive (cf. DAMAS, 1935, BALABAI, 1946 and JOHNELS, 1948), apart from the muscles which in the adult collaborate with the trigeminal musculature in the piston mechanism. These muscles are discussed on page 416.

Among the facialis branches we shall not deal further with r. recurrens and r. sympathico-branchialis, as the similarity between these nerves in Ammocoetes and in the adult is obvious. In Ammocoetes and in the adult r. hyomandibularis gives off motor branches to mm. constrictores and cutaneous branches running rostrad. In addition, it gives off the following two branches caudad. A branch runs in the subcutis to the area rostral to the first external branchial aperture, where it unites with a branch of r. cutaneus descendens. The other branch pierces the constrictor musculature and divides on the

medial side of the latter into branchial nerve bundles, one running caudad to the first external branchial aperture and one running caudo-ventrad down towards the thyroid. This latter bundle is identical with ALCOCK's "r. thyroideus" in Ammocoetes (1899) and JOHNSTON's ventral sympathetic nerve in the adult (1908 a). The dorsal branchial nerve bundle probably carries both motor and sensory fibres destined for the gill musculature and part of the mucous membrane on the anterior half of the first gill sac. The ventral bundle in all probability contains similar fibres and, in addition, fibres to blood vessels and the thyroid. The terminal distribution of the branchial nerve bundles are difficult to trace, particularly in Ammocoetes, and statements regarding their peripheral destination in the present material are a combination of observation and surmise. JOHNSTON's (1905) and TRETJAKOFF's (1927 a) investigations seem to have proved that r. sympathico-branchialis belongs to the autonomic (and to the visceral afferent system?). The facialis branch running caudad along the thyroid probably also contains autonomic or visceral afferent fibres. Both it and r. sympathico-branchialis extend through several branchial segments, a fact indicating that they are autonomic.

For the innervation of the skin caudal to the eye, see page 380.

The course of r. buccalis, which passes lateral to the V_2-ganglion, dorsal to r. subopticus and—further distal—lateral to and close up against n. ophthalmicus, is similar in Ammocoetes and in the adult. The character of the commissure between the facialis and the trigeminus is uncertain, and the relation between the commissure and n. trochlearis varies to a certain extent from specimen to specimen in the adult, but one nevertheless may compare this relation in Ammocoetes to that in the adult.

The observations made on the innervation of the neuromasts in the present Ammocoetes material are far less comprehensive than the parallel observations in the adult, but no facts observed appear to indicate that the two stages differ concerning the innervation of the neuromasts.

During the metamorphosis, the extra-hyal develops caudal to r. hyomandibularis (JOHNELS, 1948), i.e. lateral to the branchial nerve bundles of the hyomandibularis and medial to the branch of the hyomandibularis joining r. cutaneus descendens.

In summarising, it may be said that a comparison of the ramification pattern and the course of the nerves in Ammocoetes to those in the adult is possible for n. facialis and most of the sensory trigeminal branches, whereas fewer similarities are found in the case of the motor trigeminal branches. This is only to be expected as the trigeminal musculature is almost completely broken down during the metamorphosis, whereas, although the larger part of the facialis musculature and the skin and mucous membrane areas containing the peripheral endings of the sensory trigeminus and facialis branches are

certainly changed during the metamorphosis, the transformation is not so radical that the structures in Ammocoetes are broken down in order to make room for the adult structures.

VII. FIBRE CALIBRE. RAMIFICATION TYPES OF THE SENSORY AND MOTOR BRANCHES.

Data on the calibre of the fibres are intended in the first place to give an idea of the accuracy with which the various types of fibres in a mixed nerve can be distinguished. The measurements given must be judged with a certain reserve as the calibre appears to vary with the fixing conditions in the fibres. The ratios between the various calibres are more important than the absolute values.

The calibre of the trigeminal fibres is more even throughout in Myxine than in Petromyzon. Most of the sensory fibres are finer than the motor ones. The diameters of the sensory fibres are 0.5—2 μ and of the motor fibres about 3 μ. There are, however, in the sensory bundles isolated fibres as thick as 3 μ or more.

The calibre of the fibres in the branch of rr. velobuccales joining r. muscularis posterior and in the branches running from the mixed nerve to the mucous membrane of the buccal cavity ... 0.5—1 μ
The calibre of the fibres entering the tendon of m. clavatus ..... 3 μ
The calibre of the fibres running from the ganglion to r.m. craniobasalis and of the peripheral fibres from the mixed nerve which are lost in the vicinity of the basal plates ..... 0.5—1 μ

The measurements given above are taken distally in the large nerve trunks, as proximally, where the fibres are bundled more closely together, the shape of the fibres is often irregular and the calibre somewhat finer. During the passage through the brain capsule, the calibre of the motor fibres is considerably finer than further distal. The motor fibres are often more intensely stained than the sensory ones.

In the region where a muscle is innervated by a motor branch, there are fibres 3 μ in diameter and fibres only half as thick or even finer. No ramification of the thicker fibres into finer ones was observed, the transformation of the motor fibres into finer terminal branches presumably taking place more slowly than in Petromyzon (cf. fig. 42). The cutaneous fibres are as a rule difficult to trace peripherally as they are lost between the bundles of connective tissue in the cutis. The cutis contains closely packed fibre bundles of connective tissue running at right angles to one another. The nerve fibres

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Fig. 42. Petromyzon, adult. Ramification of a motor nerve fibre in m. basilaris. Transverse section. 400 ×.

make their way between the connective tissue fibres and are lost to view at the right angle bends which they appear to make.

The calibre of the motor facialis fibres is 3 μ and that of the finer fibres which are proprioceptive, visceral afferent or belong to the autonomic system, 0.5—1 μ.

Concerning Petromyzon, ALCOCK (1899) states that the differences in thickness between the nerve fibres in the sensory n. ophthalmicus are considerable, whereas all the fibres in the mixed n. vagus are extremely fine. Refering to this correct observation, ALCOCK states that she was not able to group the fibres of the cranial nerves into motor fibres and sensory fibres by means of their calibre. It is, however, possible to observe a certain regularity even in the calibre of these nerves. At the roots the variations in calibre in the trigeminal fibres are very limited. The data given below refer to adult Petromyzon.

Calibre of the motor fibres at the root	about 3 μ
Calibre of the sensory fibres at the root	1.5—3 μ
Calibre of the motor fibres in r. mandibularis and r. basilaris	3—10 μ
Calibre of the motor fibre in branches to m. pharyngeus, m. postpharyngeus and *m. vélaire descendent*	about 3 μ

Calibre of the fibres in r. perforans, r. supra- and subpharyngeus	1.5—3 μ
Calibre of the fibres in r. velaris and the sensory fibres in r. mandibularis	about 1.5 μ or less
Calibre of the fibres in n. ophthalmicus and r. suborbitalis	1.5—10 μ
Calibre of the fibres in r. buccalis and n. lateralis posterior	3 μ

JOHNSTON (1908 a) states that the motor fibres increase in thickness before they reach the muscles. It is clear from the above, however, that only some of the motor fibres increase. It is unusual for the calibre of the motor trigeminal fibres to be less than 3 μ. The thick motor fibres are those most easily distorted during fixing. The marked variation in calibre in the fibres of r. suborbitalis and n. ophthalmicus (entirely of mainly general cutaneous fibres, fig. 43) contrasts sharply with the even calibre of the fibres in r. buccalis and n. lateralis posterior, which are presumably exclusively lateralis nerves. The calibre of the fibres in r. cutaneus descendens and r. recurrens facialis varies between 1.5 and 3 μ. This suggests that the nerves cannot consist entirely of lateralis fibres (cf. the discussion on these nerves in earlier chapter).

P. fluviatilis does not differ widely from P. planeri as regards the calibre of the fibres.

The following data refer to Ammocoetes.

Calibre of the fibres in n. facialis, n. ophthalmicus and r. mandibularis	0.5—1.5 μ
Calibre of the fibres in r. suborbitalis and motor branches from r. subopticus	about 1.5 μ
Calibre of the fibres in sensory branches from r. apicalis (r. subpharyngeus, etc.)	0.5—1 μ

ALCOCK's assertion (1899) that the nerve fibres in the muscles formed during the metamorphosis are thicker than the others appears to be correct. The musculature of the branchial region changes very little during the metamorphosis (DAMAS, 1935), and the branches of n. facialis and n. glossopharyngeus to these muscles in the adult do not contain the giant fibres to be found in r. basilaris, r. mandibularis and r. subocularis. An increase in the muscle mass during the metamorphosis is particularly apparent in the region innervated by r. mandibularis and in m. subocularis. A count of the nerve fibres in r. mandibularis also shows straight away that a number of new nerve fibres must be formed during the metamorphosis; most of m. subocularis is a new formation (cf. p. 418). Only study of the metamorphosis, however, can decide whether the thick fibres in the adult really are new formations. It is

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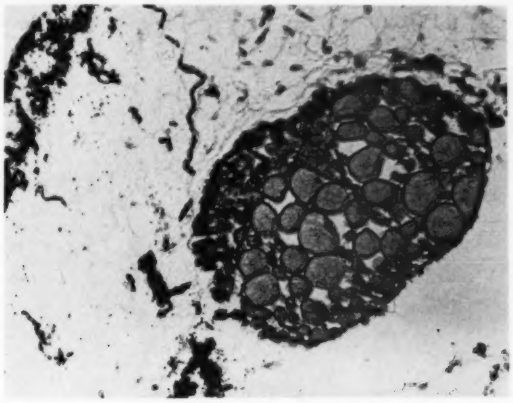

Fig. 43. Petromyzon, adult. Variations in calibre in n. ophthalmicus. Part of the nerve pictured is r. buccalis (left). Transverse section. 290 ×.

of course possible that the new fibres are thin and that the thick fibres in the adult arise as the result of a thickening of the already existing fibres in Ammocoetes.

The motor fibres in the adult normally run in a single bundle to a muscle. Once inside the muscle, the motor bundles suddenly ramify and each fibre splits up into a number of considerably finer terminal fibres (fig. 42). The sensory nerves, on the other hand, ramify slowly in several branches running parallel in the the subcutis, skin or the mucous membranes, branches which send out from time to time fibres or bundles of fibres to the epithelium.

VIII. VARIATIONS IN THE COURSE OF THE CRANIAL NERVES.

Data given in the literature on the Cyclostomes indicate that several systems of organs in these fish are subject to a certain variation. There are two reasons for discussing the variations in the nervous system in greater detail here. The first is that there are some deficiencies in the present material (see p. 318), and the other that the variations concern important relationships affecting the discussion (p. 436).

In Myxine the manner in which the motor nerve to m. levator cartilaginis basalis passes the branches of r. externus varies (p. 348). This variation has been linked up on page 352 with the course of a branch of r. externus in an aberrant specimen. R. dentalis can pass m. flexor trabeculae in various ways (p. 344). The buccalis ganglion may be well or less well delimited from the trigeminal ganglion (p. 355). An independent proximal facial ganglion is found only in certain specimens, whereas it is probably incorporated in the utricular ganglion in others. The variations in the buccalis and facial ganglia may, however, be presumed to arise during a late stage in the ontogenesis. The facial nerve has an aberrant course in one specimen while passing r. mm. protractores

dentium (p. 359). In this specimen the nerve contains some cell bodies peripheral to the normal extension of the facial ganglia, and the branch containing these cell bodies passes m. protractor cartilaginis basalis anterior in an abnormal way. Finally, it may be mentioned that n. ophthalmicus and r. muscularis posterior can be divided proximally into two or more branches which more distally reunite (pp. 333 and 349).

The variations in the nervous system in Petromyzon appear to affect more important relationships than do the variations in Myxine. In one half of the body in an aberrant specimen of Ammocoetes, r. subpharyngeus runs at its origin through r. subopticus; in the other half of the body, and in the other specimens studied, r. subpharyngeus is given off from the medial side of r. subopticus (p. 374). In the adult the relation between n. trochlearis and the commissure uniting the facial ganglion and the ophthalmic ganglion varies (p. 392). In one half of the body in two adult specimens n. abducens passes between the motor and the sensory trigeminus out to the orbit. In the other half of the body in these specimens, and in the other specimens studied, n. abducens passes between the V_1-ganglion and the V_2-ganglion out to the orbit (p. 396). In one half of the body in an adult specimen, r. velaris emerges from the lateral part of the V_2-ganglion, whereas it is given off from the medial part of the ganglion in the other half of the body and in the other specimens studied (p. 378). Variations in the course of a number of small bundles of fibres in the region where the facial and trigeminal ganglia are situated in the adult are mentioned on page 368. The course of r. recurrens rami apicalis varies in the adult as regards the muscles passed through (p. 384). R. mandibularis passes through the cornual cartilage in a variable manner (p. 377). R. cutaneus descendens leaves the V_2-complex as one or two branches both in the adult and in Ammocoetes (p. 404). The branch of the facialis which joins up with r. cutaneus descendens varies in size in the adult (p. 391). The relation between the most anterior spinal nerves and the most anterior spinal skeletal arch varies in the adult (p. 402).

Finally, it may be mentioned that whereas the course and ramification of the two main trunks of n. ophthalmicus and the four main trunks of r. externus are relatively constant in Myxine, the ramification patterns of n. ophthalmicus, r. suborbitalis, r. suprapharyngeus and the skin branches of r. hyomandibularis vary in (adult) Petromyzon. The Petromyzon nerves in question run to a great extent subcutaneously, and it is during the subcutaneous course that the ramification patterns differ. In Myxine, the nerves in question run for the greater part of their course embedded in the trigeminal musculature.

According to KOLTZOFF's description of the embryonic development of Petromyzon (1902), the three somites which are to develop into eye muscles are formed in a rather medial position whereas the trigeminal ganglia and their nerves start to develop more laterally. KOLTZOFF describes on page 349

how the mandibular myotome migrates laterad during the embryonic development. There is reason to suspect that the variation in the relation between n. trochlearis and the commissure uniting the facial and the trigeminal ganglia is due to the mandibular myotome passing the said commissure in varied ways during its migration. A similar situation may be the reason for the varying course of n. abducens in Petromyzon and the varying course of r. m. levator cartilaginis basalis in the Myxinids. In the latter case, the primordium of the muscle might migrate laterad during the embryonic development, passing r. externus in various ways. These explanations are, of course, purely hypothetical.

It is clear from the above account that the variations in the nervous system affect chiefly the ramification patterns and the way in which the nerves cross one another. It was not possible in a single case in the present material to observe in aberrant specimens nerve branches to the muscles—defined by their roots and their peripheral termination—which join branches to the skin or the mucous membrane which they do not join in normal specimens.

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IX. THE MUSCULATURE.

1. THE TRIGEMINUS AND FACIALIS MUSCULATURE.

The musculature has not been studied exhaustively in the present work. Some additions will, however, be made to the descriptions given by P. FÜRBRINGER (1875), TRETJAKOFF (1926a, 1929a) and DAMAS (1935).

We shall first give a summary of previous works on the piston mechanism. The piston mechanism consists of antagonistic muscles attached to the tooth plate cartilage in Myxine and to the apical cartilages in Petromyzon. The muscles all run parallel, and all have their origins caudally and their insertations rostrally. The dorsal antagonist is m. clavatus in Myxine and m. cardio-apicalis in Petromyzon. This dorsal antagonist is surrounded by a tube-shaped muscle: m. tubulatus in Myxine and *m. infravélaire posterieur* in Petromyzon. *M. vélari-apical* assists m. cardio-apicalis in Petromyzon. The ventral antagonists are mm. protractores dentium in Myxine, whereas Petromyzon has only one: m. copuloglossus obliquus. The antagonistic effect is achieved in Myxine by the tendon of mm. protractores dentium bending dorsad and caudad, running over the rostral edge of the basal plates. The same effect is achieved in Petromyzon by m. copuloglossus obliquus changing at a point dorsal to m. spinosocopularis into a tendon which bends dorsad, running rostral to (according to FÜRBRINGER, piercing) a ligament which connects indirectly the medioventral cartilage and the anterior lateral plate (see below). After this the tendon of m. copuloglossus obliquus is inserted on the top of the lateral apical

cartilage. The tendon from *m. vélari-apical* joins up with its antimere and with the unpaired tendon of m. cardio-apicalis in Petromyzon and the thus united tendon divides further rostrally into a tendon on each side of the medial line, and these tendons are inserted both at the top of the lateral apical cartilage and in the anterior lateral apical cartilage.

The above description has been known in the main since P. FÜRBRINGER (1875). Through the work of HOLMGREN—STENSIÖ (1936) and JOHNELS (1948) we know that the lateral apical cartilage is joined in Petromyzon to an unpaired medial cartilage and that this in its turn is joined by soft cartilage to the piston cartilage. This soft cartilage appears to function as a hinge during the movement of the apical cartilages. (Cf. REYNOLDS, 1933.) The tooth plate cartilage in Myxine is, on the other hand, free to move independently of other cartilages. HOLMGREN (1946) homologizes, however—with a certain reserve—the tooth plate cartilage in Myxine with the cornual cartilage in Petromyzon. It is clear from JOHNELS's paper (1948) that this comparison is not supported by the relations between the cartilages and the nerves because the tooth plate cartilage is pierced by sensory branches from r. dentalis whereas the cornual cartilage in Petromyzon is pierced by motor branches from r. mandibularis.

HOLMGREN (1946) found in a Myxine embryo the primordia of mm. protractores dentium, m. clavatus and m. tubulatus. In Petromyzon the musculature of the piston mechanism does not develop until the metamorphosis which involves radical changes in this region. The homology given above between the piston mechanism in Petromyzon and in Myxine is difficult to confirm by ontogenetic studies and the problem is closely linked up with the discussion on the phylogenetic significance of the organisation of Ammocoetes and the adult, respectively.

The innervation of the ventral antagonist(s) takes place in Myxine by means of r. muscularis posterior and in Petromyzon by means of the rostrally directed r. basilaris. The dorsal antagonist is innervated in Myxine by r. muscularis posterior and in Petromyzon by r. mandibularis, both of which nerves run mainly ventro-caudad. In additon, a nerve of uncertain character enters the tendon of the dorsal antagonist and is partly lost there but can partly be traced to the muscle tissue. This nerve, whose distal course is similar in Myxine and Petromyzon, originates in Myxine from r. muscularis posterior which runs ventro-caudad (see p. 344) but in Petromyzon from r. apicalis which runs rostrad (p. 384).

If, on the basis of the main direction of the nerve trunks in the Cyclostomes, one attempts to draw a boundary between a r. maxillaris and a r. mandibularis, a homology between the piston mechanism in the two groups of the Cyclostomes is difficult to establish. Only by treating the motor and sensory V_2-complex as units is it possible to compare the piston mechanisms of Myxine and Petro-

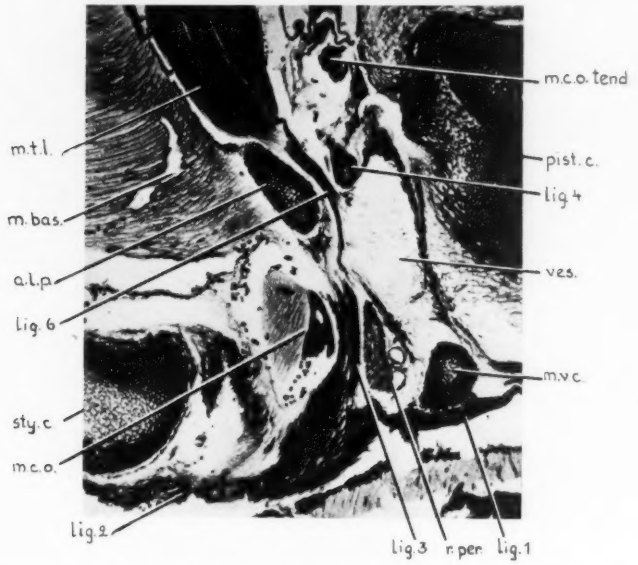

Fig. 44. Petromyzon, adult. Some ligaments in the rostral part of the head. "m. bas" is a complex, formed by m. basilaris and m. tectospinosus posterior. Transverse section. 60 ×.

myzon. In view of the obvious similarity between the mechanisms, such an alternative is preferable.

The ligaments in the rostral part of Petromyzon are of some interest. A ligament (1) forms a rostral continuation of the medio-ventral cartilage. The ligament is horizontal and in its turn connected by ligaments to:

the fascia on mm. tectospinosi and the stylet cartilage (ligament 2);
the anterior lateral plate (ligament 3);
the base of the lateral apical cartilage (ligament 4);
the tendon of m. tectolateralis (ligament 5).

Ligament No. 5 lies caudal to ligaments 2—4. No direct ligament connection between m. tectolateralis and the anterior lateral plate could, however, be found in the present material.

R. perforans passes dorsal to ligament (1) and medial to this ligament's four connections (cf. fig. 44). Rostral to the ligaments, the nerve bends ventrolaterad out towards the annular cartilage. The rostral part of the piston cartilage lies in a gutter-shaped structure of vesicular supporting tissue (cf. JOHNELS, 1948, fig. 57 and p. 235). Ventrally the structure changes gradually into the cartilage of the medio-ventral cartilage, and lies medial to n. perforans. The gutter-shaped structure is surrounded by regular connective tissue and forms the insertion of two ligaments: No. 6 running to m. tectolateralis, caudal to ligament 4, and No. 7 running to the anterior lateral plate and the

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fascia of m. tectospinosus posterior, rostral to ligament No. 4. The tendon of m. copuloglossus obliquus slides over ligament No. 7.

The facialis musculature consists in the Cyclostomes partly of a muscle which is an immediate cranial continuation of the gill basket musculature of the vagus group (pharyngeal basket musculature in the Myxinids), and partly of a group of muscles connected to the piston mechanism. The first muscle lies caudal to the large curve in r. hyomandibularis and is called m. constrictor branchialis externus I in Petromyzon and m. cranio-hyoideus in Myxine. The muscle group consists of *m. infravélaire inféricur* and *m. vélaribranchial* in Petromyzon. These are attached to the extra-mandibular and the cornual cartilage, and to the ligament and cartilage ventral to the piston mechanism. This recalls the arrangement of mm. protractores cartilaginis basalis in Myxine, which at least to some extent have their origin in the extra-mandibular and their insertion on the basal plates.

HOLMGREN (1946) compares the muscle groups which he observed in Myxine embryo to the muscle groups described by SEWERTZOFF (1917) in young Ammocoetes, comparing a hyoid group in Myxine to "constrictor and adductor praebranchialis I" in Ammocoetes. According to TRETJAKOFF (1927 a) these muscles in Ammocoetes are transformed during the metamorphosis into m. constrictor branchialis externus I. However, TRETJAKOFF has overlooked the fact that *m. vélaribranchial* and *m. infravélaire inféricur* are facialis innervated. He states that these muscles develop out of the velar group, and the velar group belongs to the trigeminal region. TRETJAKOFF'S comparison between the trigeminal musculature in Ammocoetes and that in the adult has been sharply criticized by DAMAS (1935), who could not find any continuity between the trigeminal muscles in Ammocoetes and those in the adult. DAMAS has not noticed TRETJAKOFF'S mistake, mentioned above, regarding the innervation of *m. infravélaire inféricur* and *m. vélaribranchial*. JOHNELS (1948, p. 216) states that *m. vélaribranchial* develops out of a blastema coming from "the mesenchyma formed by the dissolved pharyngeal musculature in this area". It is uncertain which muscle "the pharyngeal musculature" refers to. It must be either *m. constricteur buccal* (a trigeminal muscle) or m. constrictor praebranchialis (a facialis muscle). Under the circumstances, it may be stated that the data obtained hitherto from Petromyzon embryogeny and metamorphosis do not argue against the comparison between the facialis musculature in Petromyzon and Myxine suggested by the present writer. It should be added that mm. protractores cartilaginis basalis is displaced rostrad during the ontogenesis of the Myxinids from a position close against the musculature of the pharyngeal basket to the position the protractors occupy in the adult, where they collaborate with the musculature of the piston mechanism (p. 323).

No observations on the peripheral course of n. facialis and n. trigeminus or

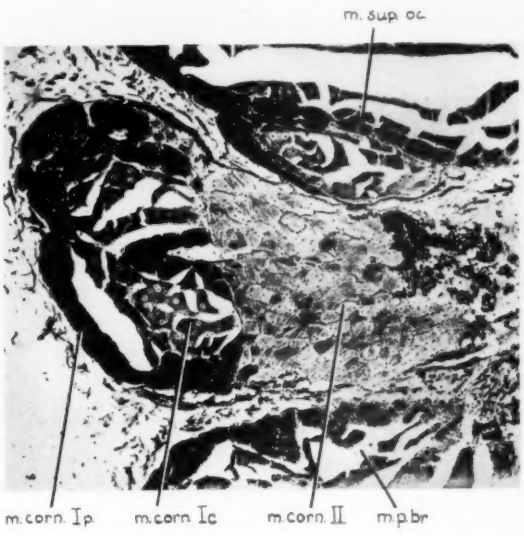

Fig. 45. Petromyzon, adult. Transverse section through m. cornealis. The spinal part of the muscle lies laterally. 55 ×.

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of the muscles innervated by these nerves appear to support ADDENS's (1933) hypothesis that some of the motor fibres, which in Petromyzon run in n. facialis, are to be found in n. trigeminus in Myxine.

2. THE SPINAL MUSCULATURE.

HATSCHEK (1892) states that m. cornealis (which he called m. rectus oculi externus) has a "Kästchenstruktur". TRETJAKOFF (1926 a, 1927 a) writes that the muscle certainly resembles the spinal musculature in as much as it has two segments, separated by a myoseptum, but maintains that it lacks "Kästchenstruktur" and consists instead of "einzelne Muskelfasern". "... die sich von den übrigen vom N. trigeminus versorgten muskeln nicht unterscheiden." TRETJAKOFF (1929 b) considers that m. cornealis and m. obliquus posterior constitute a remnant of a fourth prootic myotome.

PALMGREN's (1948) method of staining is particularly suitable for bringing out the difference between parietal and central muscle fibres in the "Kästchen" of the spinal musculature (cf. STANNIUS, 1851, and MARCUS, 1925). The existence of central and parietal muscle fibres in the lateral part of m. cornealis is very clearly seen in a series of P. fluviatilis stained by this method (fig. 45). The lateral part of m. cornealis is thus constructed like the spinal musculature. The medial part of m. cornealis is, on the other hand, of the same type as the special visceral musculature in the head. M. cornealis is thus a composite muscle. The two components exist in all the specimens studied, but differ in importance in the various parts of the corneal muscle. As was

mentioned on page 378 m. cornealis is not innervated by the trigeminus. The spinal part of the muscle is in all probability innervated by the most anterior ventral spinal nerve trunk, i.e. by the rr. ventrales of the first and second spinal nerves (cf. pp. 400 and 402). It is difficult to give an account of the innervation of the medial part of m. cornealis. Single motor fibres enter the muscle at a number of places. There is, however, no real motor nerve branch entering the medial part of m. cornealis. N. postorbitalis normally pierces m. cornealis and it is possible that the nerve carries glossopharyngeal fibres to the muscle, but it is also possible that n. facialis (r. recurrens??) gives off motor fibres to the medial part of m. cornealis.

In Ammocoetes, r. cutaneus descendens runs between *la portion latérale des myomères épitrématiques* and the most anterior part of *les myomères hypotrématiques*. R. hyomandibularis pierces the most anterior part of *les myomères hypotrématiques*, and r. suborbitalis runs out to the subcutis a certain distance rostral to the front edge of the muscle, ventral to the most rostral part of *la portion latérale* etc. The most anterior ventral spinal nerve trunk (belonging to two spinal segments) innervates *la portion latérale* etc. and in doing so passes lateral to r. cutaneus descendens. The innervation of the rostral hypotrematic myomeres is difficult to ascertain. The most rostral part is, however, innervated from the most anterior ventral spinal nerve trunk, and the fibres innervating this rostral part appear to pass both lateral and medial to r. cutaneus descendens. In the adult, r. cutaneus descendens passes between m. praebranchialis and the posterior part of m. subocularis. R. hyomandibularis pierces the posterior part of m. subocularis dorsally. R. suborbitalis passes dorsal to the anterior part of m. subocularis. The most anterior ventral spinal nerve trunk (belonging to two spinal segments) innervates m. cornealis and m. praebranchialis, but gives off in addition the powerful r. subocularis and r. posthyoideus which pass medial to r. cutaneus descendens and innervate m. subocularis (cf. TRETJAKOFF, 1927 a). The relations between the nerves and the muscles in Ammocoetes and in the adult are explained by DAMAS' description (1935) of how *la portion latérale* etc. develops into m. praebranchialis and m. cornealis during the metamorphosis and how m. subocularis develops out of a primordium that is embryonic in character throughout the entire Ammocoetes period. That motor spinal nerve branches pass lateral to r. cutaneus descendens in Ammocoetes but not in the adult, is due to the fact that r. cutaneus descendens in Ammocoetes passes medial to the *central* part of *la portion latérale* etc. whereas in the adult it runs medial to the *most rostral* part of m. praebranchialis. R. subocularis does not exist in Ammocoetes and is thus a new formation in adult Petromyzon. Part of the problem, nevertheless, still remains unsolved. R. cutaneus descendens passes dorsal to, and r. hyomandibularis pierces, the most anterior part of *les myomères hypotrématiques* in Ammocoetes. In the adult, the nerves have the same rela-

tion to the posterior part of m. subocularis. Presumably the posterior part of m. subocularis—the part innervated by r. posthyoideus—is not newly formed during the metamorphosis but results from the growth of the rostral part of *les myomères hypotrématiques* in Ammocoetes. This assumption is strengthened by the fact that the rostral part of *les myomères hypotrématiques* in Ammocoetes is innervated by the most anterior ventral spinal nerve and not by n. hypoglossus. As the author has not studied metamorphosis material, this comparison cannot be established with certainty. It seems, however, probable that the muscle, the formation of which during the metamorphosis, out of a primordium is described by DAMAS, is really only the anterior part of m. subocularis—the part innervated by r. subocularis. (Cf. TRETJAKOFF, 1927 a, figs. 8 and 11.) DAMAS may have misinterpreted TRETJAKOFF'S definition of m. subocularis since DAMAS mentions m. subocularis as "une lame musculaire triangulaire"—such a description is true of only the anterior part of m. subocularis.

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X. THE RELATIONS BETWEEN N. TRIGEMINUS AND THE CRANIAL BLOOD VESSELS.

CORI (1906), HATTA (1923) and CLAYDON (1938) have described the morphology and the embryonic development of the vessels in Ammocoetes. JOHNELS (1948) has given some data on the vessels during the metamorphosis, and TRETJAKOFF (1926 b, 1927 b) has given an account of the vessels in adult Petromyzon. The blood vessel system in some embryonic stages of the Myxinids has been described by NEUMAYER (1938) and HOLMGREN (1946). For the vessels in adult Myxinids compare COLE (1926) and GRODZIŃSKI (1927). References to the earlier literature on the subject are given in the works mentioned.

It might be expected that the relations between the trigeminal branches and the blood vessels would offer facts of considerable importance in comparing the Myxinids and the Petromyzonids. The vessel anatomy of the Cyclostomes is, however, very difficult to interpret, one of the contributary factors being that sinus formations are rather common in the adult Cyclostomes and appear partly to replace the veins. Some examples will illustrate the difficulties presented by a comparison between the blood vessel systems in the Myxinids and the Petromyzonids. The mandibular aortic arch in Petromyzon undergoes a very unusual embryonic development and is introduced into the venous system (cf. HATTA). The existence of a praemandibular aortic arch in Petromyzon may be said to be the core of the present discussion (cf. CLAYDON). The most anterior aortic arches are entirely unknown in the Myxinids. HOLMGREN interprets "the external carotid" (COLE) in Myxine as an aortic arch (the third or the fourth) plus a lingual artery. Although HOLMGREN does

not actually say so, the "external carotid" should contain in addition a part corresponding to carotis ventralis (CORI) in Ammocoetes and the adult Petromyzon's parabranchial artery (TRETJAKOFF, 1927 b), respectively. The lingual artery exhibits certain similarities to the lingual artery in Petromyzon. No attempt has been made to compare in detail the carotides (the internal carotides) and their branches in the Myxinids and the Petromyzonids. HOLMGREN has shown great differences between the venous system of the Myxine embryo and the adult Myxine—differences which cannot at present be more than partially bridged. A vena capitis lateralis is described in Ammocoetes (CORI, HATTA) and in Bdellostoma embryo (NEUMAYER), but HOLMGREN does not confirm the existence of such a vein in Myxine embryo. In the position where NEUMAYER describes a v. capitis lateralis, the subcutaneous anastomosis (COLE) runs in the adult Myxine. If we exclude the cerebral veins (COLE), then the cardinal heart medial to the extra-hyal represents in adult Myxine the rostral termination of the veins proper. In order to discuss the vein-sinuses lying rostrad to the cardinal heart, a knowledge of their ontogenesis is necessary.

In Ammocoetes the vessels of the head are easily comprehended because of the absence of sinus formations. The vessels appear to be grouped into three systems: one for the velum, one for the progressively developed brain, and one for the similarly progressively developed snout region. (CORI, 1906. Cf. ALLIS's, 1924 a, 1926 and 1938, and DE BEER's, 1923, pp. 279—281, more detailed discussions of the morphogenesis of the head in the Cyclostomes.) The V_2-complex is, of course, similarly joined to the velum and the snout region, and also reflects in its form the progressive development of this regions (p. 440). The vessels which appear to be possible landmarks in the anatomy of the V_2-complex are v. spiraculi and the vessels connecting the arteria and vena facialis mutually, and to a. lingualis. The present writer must, however, refrain from further discussion on this point, as our knowledge of the rostral vessels in the Myxinids is, as has already been pointed out, far from complete.

Some arteries will be discussed further on p. 433.

XI. THE COMPONENTS OF THE TRIGEMINUS.

1. THE MYXINIDS.

From studies of the medulla oblongata in Myxine, HOLMGREN (1919) and JANSEN (1930) state that n. ophthalmicus contains a general cutaneous component and possibly (HOLMGREN) an acustico-lateralis component, whereas the V_2-complex contains a visceral motor and a general cutaneous component. According to AYERS—WORTHINGTON (1908 a, b, 1911) a general cutaneous component is present in n. ophthalmicus and in the V_2-complex, and a visceral

motor component in the V_2-complex in Bdellostoma. They also state that, in addition, a lateralis component and a fasciculus communis component join "the anterior" ("first") and "posterior" ("second") sensory V trunk in Bdellostoma. The posterior trunk is the nerve referred to here as n. buccalis. It was already pointed out in the discussion on the components of the ophthalmicus (p. 335) that it is not possible by means of AYERS—WORTHINGTON'S data to decide how the components in the "anterior trunk" are divided between n. ophthalmicus and r. externus. The lateralis component will not be dealt with here (see p. 442). As has already been pointed out many times in this and in earlier papers, the similarity between Myxine and Bdellostoma is very great. How then is such an important difference as the presence in one animal and the absence in the other of a fasciculus communis (fasciculus solitarius) component in the trigeminus and the buccalis to be explained? The data known regarding the embryonic development of the Myxinids are of no assistance here, since the bucco-pharyngeal plate disappears at an early stage and its position cannot be traced in later stages (cf. DEAN, 1899, v. KUPFFER, 1893—1900). It is hardly likely in any case that Myxine and Bdellostoma should differ as regards the position of the bucco-pharyngeal plate. Even if we assume that the trigeminus in the Myxinids is at a primitive stage of the phylogenetic development, a stage in which the trigeminus contains a visceral sensory component destined for the most anterior part of the entodermal digestive tract, this still scarcely explains the existence of a visceral sensory component in n. buccalis.

If taste buds (end buds) occur in the skin of the Myxinids, then differences in their distribution would explain the differences in the trigeminal components in Myxine and Bdellostoma. It is, however, very doubtful whether end buds exist in this group of animals. SCHREINER (1919, p. 57) writes: "Die Sinneszellen der Epidermis . . . sind teils in Sinnesknospen und Sinneshügeln gesammelt, die besonders in der Epidermis der Nasen- und Mundfühler in grosser Zahl vorkommen, teils treten sie auch vereinzelt in der Epidermis der Körperhaut auf." The description refers to Myxine. Like RETZIUS (1892), SCHREINER stresses the similarity between these organs and the taste buds in the mouth of the Gnathostomes and those in the skin of aquatic Gnathostomes, but SCHREINER also points out a difference: these sense organs in Myxine do not reach down to the base of the epithelium whereas the sense organs in the Gnathostomes do. AYERS—WORTHINGTON (1908 a) describe sense organs in the area of the skin which is trigeminus innervated, but these organs are less like end buds. It must be pointed out here that the facialis does not innervate the skin, or the mucous membrane of buccal cavity and pharynx in Myxine, and that n. glossopharyngeus—in so far as such a nerve can be said to exist—only innervates the mucous membrane of the gut caudal to the velum in the Myxinids (cf. WORTHINGTON, 1906. Cf. also p. 361 in the present paper).

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According to JANSEN (1930), who studied the nuclei of n. glossopharyngeus in the medulla of Myxine, the nerve probably contains in addition to visceral components a lateralis and a general cutaneous component. JANSEN appears, however, to doubt somewhat the accuracy of the statement and expresses himself hesitatingly. It cannot therefore be said to be established that the nerve contains any branches destined for the skin. On the other hand, the skin on the tentacles is innervated by n. trigeminus in the Myxinids and the sense organs concerned are particularly abundant on the tentacles. If the sense organs really are end buds, the existence of a fasciculus communis component in the trigeminus of the Myxinids would be explained—one is of course forced to assume that Myxine and Bdellostoma are similar in this respect. Should this be the case, however, the innervation differs radically from that of end buds in the Gnathostomes. End buds in the Gnathostomes—whether they be interoceptive or exteroceptive—are innervated by the facialis, the glossopharyngeus or the vagus. Exteroceptive end buds are, according to ARIENS KAPPERS *et alii* (1936), innervated solely by n. facialis. Finally, sense organs in the mucous membrane of the buccal cavity in the Myxinids are unknown. It appears to the present writer scarcely probable that the sense organs in the skin of Myxine described by SCHREINER are end buds.

There exist in Myxine fibres which follow r.m. cranio-basalis and are either proprioceptive or visceral afferent (from blood vessels) or belong to the autonomic system (p. 345) and fibres which join r. muscularis posterior and are possibly proprioceptive (p. 344). The question arises whether it can possibly be fibres of this type which certain writers, who studied the medulla, describe as a contribution from the fasciculus communis system to the trigeminus. The trigeminal musculature is visceral in development but histologically and functionally of the same type as the somatic musculature, a fact which led HERRICK (1922, 1943) to state: "This difference in nomenclature is a matter of small importance, for the muscles do occupy an ambiguous position ... The essential thing is the recognition of their *special* character, in contrast with both the general visceral and the typical somatic neuromusculature systems". RANSON CLARK (1947, p. 201) draws attention to the conflict which arises if the proprioceptive fibres in the trigeminus are classified as somatic sensory together with the proprioceptive fibres from somatic muscles, as is in fact usually done. The conflict might be solved by the adoption of a system of classification analogous to that recommended by HERRICK for the motor trigeminal system.

The centres of the proprioceptive fibres in the brain of the Cyclostomes are unknown. No radix mesencephalicus exists in the trigeminus of Cyclostomes (cf. JANSEN, 1930, HEIER, 1948). It is possible to envisage that the nuclei of the proprioceptive component in the cranial nerves lie in the cerebellum. PEARSON (1936), LARSELL (1947 a) and HEIER (1948) describe primary and secondary trigeminal fibres running to the cerebellum in Petromyzon, and HOLMGREN

(1919) describes sensory trigeminal fibres running to the cerebellum in Myxine. According to JANSEN, the latter fibres are secondary and come from the general cutaneous nucleus in the medulla of Myxine. Judging from JANSEN's and LARSELL's investigations, the fibres end, moreover, in the mesencephalon and not in the cerebellum. (Regarding the existence of a cerebellum in the Myxinids cf. CONEL, 1929, 1931, JANSEN, 1930, HOLMGREN, 1946, and LARSELL, 1947 a.) Assuming a correspondence to exist between the nuclei in the two groups of the Cyclostomes, these data on the central nervous system certainly do not indicate the existence rostral to the medulla of nuclei belonging to primary proprioceptive neurons. The possibility of the existence of such a centre in the fasciculus communis nucleus in the medulla has been discussed in connection with n. facialis in Myxine (p. 360). Several unsolved problems resulting from such an assumption were pointed out there. The situation is equally confusing in the region of the peripheral nerves. The present writer has had reason to suspect that two trigeminal branches carry proprioceptive fibres in Myxine. One branch has fine fibres and emerges together with the sensory trigeminal component. It is uncertain whether these fibres come from cell bodies in the ganglion. The other branch is made up of thick fibres, emerges together with the motor component and definitely contains no extracerebral cell bodies. Proprioceptive end organs have been described by STEFANELLI (1932) in Petromyzon's musculature and tendons in *inter alia* the trigeminal region. The nerves of these organs apparently follow the motor trigeminal fibres. Nothing is known regarding the possible existence of such sense organs in the trigeminal region of the Myxinids, since suitable investigations have not been carried out. Judging from the conditions in Gnathostomes, there is reason to expect that the proprioceptive trigeminal fibres emerge as a single bundle. Even if v. VALKENBURG's statement (1912) that radix mesencephalicus V always emerges together with the sensory trigeminal fibres cannot be generally applied (cf. WOODBURNE, 1936), it would be surprising if both branches in question in the trigeminus of Myxine were really proprioceptive in character. It may be added that the only known proprioceptive fibres in the spinal nerves of the Cyclostomes pass through the dorsal roots in Petromyzon (JOHNSTON, 1908 a) but through the ventral roots in Bdellostoma (ALLEN, 1917). Since the situation is so confused it is inappropriate to make any definite decision regarding the character of the two trigeminal branches in Myxine. There are the following possibilities: the branch accompanying r.m. cranio-basalis may carry either proprioceptive or autonomic fibres or visceral afferent fibres (coming from blood vessels), and the branch accompanying r. muscularis posterior may carry proprioceptive or merely motor fibres. The fibres accompanying r.m. cranio-basalis are few and very fine. It is not out of the question that it is such fibres which AYERS—WORTHINGTON describe as a fasciculus communis component in the trigeminus of Bdellostoma.

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2. THE PETROMYZONIDS.

According to JOHNSTON (1902, 1905, 1908 a), the components in the trigeminus of Petromyzon are general cutaneous and visceral motor. SCHILLING (1909) and SAITO (1930) do not use JOHNSTON's terminology, but their anatomical descriptions agree well with his. PEARSON (1936), WOODBURNE (1936) and BARNARD (1936) confirm JOHNSTON's data. The lateralis character of the commissure from the facial ganglion is discussed on page 388. JOHNSTON (1908 a) discusses the possibility that r. velaris contains a communis component, basing his arguments upon the fine calibre of the fibres and the smallness of the cell bodies. He says (p. 607): "The central connections of the fibers were not impregnated". In a later paper, however, he states (1908 b, p. 616): "... the general cutaneous system, to which, so far as we know, the fibers of the velar nerve belong." No small-celled group in the V_2-ganglion of the adult has been found in the present material. In Ammocoetes the cell bodies in the medial part of the ganglion are on an average smaller than in the lateral part, but the small cell bodies belong not only to r. velaris but also to other larger nerves.

This, however, is not in itself sufficient to dismiss the possibility of the existence of visceral sensory fibres in the trigeminus. MERKEL (1880), JOHNSTON (1902), RAZZAUTI (1917) and FAHRENHOLZ (1936) describe some sort of "end buds" in the skin of adult Petromyzon. They state that the sense organs are found over the entire surface of the body but are concentrated in the cephalobranchial region. The organs are, however, said to be absent in the buccal cavity. RAZZAUTI and FAHRENHOLZ point out that the structure of the sense organs differs widely from that of the end buds in Gnathostomes and from end buds on the branchial diaphragma in Ammocoetes and in the branchial duct of adult Petromyzon. (The latter type of sense organs is discussed by FAHRENHOLZ only.) FAHRENHOLZ is very doubtful about the homology between the sense organs in the skin of Petromyzon and end buds. It may be pointed out here that the structure of the neuromasts in Petromyzon differs, according to RAZZAUTI, from that of the neuromasts in the Gnathostomes, but that this difference is denied by FAHRENHOLZ. RAZZAUTI states that the "end buds" in the skin of Petromyzon are at least partly innervated by n. glossopharyngeus and n. vagus. He also states that the organs are particularly concentrated in the skin of the ventral part of the head and in the branchial region. This makes it likely that n. facialis also takes part in the innervation of the sense organs. On the basis of the available data on the existence of the sense organs one can, moreover, presume that a small number are innervated by n. trigeminus. This would imply that the trigeminus of Petromyzon contains a visceral sensory component, assuming of course that the sense organs really are end buds.

Finally, mention should be made of the trigeminal branch which is lost close to *m. infravélaire postérieur* (p. 377). Nothing is known of the components of this branch, but it is probably proprioceptive, visceral afferent (coming from blood vessels) or autonomic in character.

3. THE "END BUDS" IN THE CYCLOSTOMES. SUMMARY.

The structure of the "end buds" in the skin of the Cyclostomes argues against a homology between these sense organs and the end buds in the Gnathostomes. The innervation of the "end buds" in Myxine also argues against such a homology. The innervation of the sense organs in the skin of Petromyzon is more similar to that of the end buds in the skin of the Gnathostomes, but even here there are considerable differences. The minute innervation differs (RAZZAUTI, 1917). The innervation of all the exteroceptive end buds in the Gnathostomes is effected by n. facialis, (ARIENS KAPPERS *et alii*, 1936, HERRICK, 1944), whereas in Petromyzon several nerves take part in the innervation. There is no differentiated taste centre in the visceral afferent centre in the medulla of the Cyclostomes (JANSEN, 1930, BARNARD, 1936). This is the reason why the writers dealing with the position of the motor facial nucleus (for the literature see p. 398) consider that the rostral position of the nucleus is primitive, since when a taste centre is formed in Gnathostomes, the motor facial nucleus is displaced in a caudal direction towards the taste centre—an example of neurobiotaxis. HERRICK (1944) has shown that the existence of exteroceptive end buds is accompanied by differentiations of the central nervous system rendering it possible for the animal to respond with different reactions to impulses coming from the exteroceptive end buds and impulses from the interoceptive end buds. No such differentiation has been found in the Cyclostomes. According to HERRICK, the Cyclostomes constitute a group of animals in which the isolation of the various components has not proceeded far into the central nervous system. HERRICK links this up with the fact that these animals respond to incoming impulses with mass movements, i.e. impulses from different peripheral regions give rise to a great extent to the same stereotyped effect. It is difficult to imagine mass movements which would be an appropriate response to impulses from both exteroceptive and interoceptive end buds.

As the anatomy of the medulla and the structure and innervation of the sense organs in the skin of the Cyclostomes argue against the organs really being end buds, the hypothesis ought to be abandoned and an attempt made to interpret the organs of the Cyclostomes in another way. HERRICK's arguments mentioned above render it unlikely that the central connections of these sense organs are joined to the visceral sensory system. The most probable explanation appears to be that the sense organs belong to the somatic system.

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XII. COMPARISON OF THE TRIGEMINUS IN THE MYXINIDS AND THE PETROMYZONIDS.

It was pointed out in the last chapter that the trigeminus in the Cyclostomes lacks visceral sensory branches to the skin, and the mucous membranes of the buccal cavity and the pharynx. There are thus no grounds for interpreting the rostrally directed branches of the trigeminus as a r. praetrematicus or r. pharyngeus of a segmental branchial nerve. JOHNSTON (1908 a) points out that the other cranial nerves in the Cyclostomes lack rr. praetrematici and that "r. maxillaris" (i.e. r. externus plus r. muscularis anterior in Myxine and r. subopticus in Petromyzon) is rather better identified as a r. dorsalis in the schema of a segmental branchial nerve, since the sensory elements are somatic. Motor elements are found in the maxillaris for example in Holocephali and Dipnoans (LUTHER, 1909, 1913) and in the rostrally directed trigeminal trunks in Cyclostomes; a fact which also argues against interpreting any of these nerves as a r. praetrematicus. SEWERTZOFF (1917) considers that the trigeminus in Petromyzon is a complex nerve belonging to the mandibular segment and two praemandibular segments. This would certainly explain the existence of motor fibres in the rostrally directed branches, but SEWERTZOFF's hypothesis is contradicted by TRETJAKOFF's neurologic (1927 a, 1929 a and b) and KOLTZOFF's (1902) and DAMAS' (1944) embryologic investigations. KOLTZOFF's and DAMAS' studies show that the ophthalmicus, the V_2-complex and the facialis in Petromyzon are three segmental nerves belonging to the praemandibular, the mandibular and the hyoid segments, respectively. WEDIN's investigation (1949) of Petromyzon embryos indicates that KOLTZOFF and DAMAS misinterpreted the segmental value of certain somites. WEDIN does not, however, link up his findings with other known facts effecting the interpretation of the metamerism of the head. N. mesencephalicus (TRETJAKOFF, 1909 b) has not been studied on the present material, and its significance as a segmental nerve will not be discussed here.

R. palatinus occupies to some extent an exceptional position in the trigeminal complex of Myxine. The facialis and the V_2-complex, except for one trunk of r. palatinus, pass between the neurocranium and the dorsal longitudinal bar. The dorsal longitudinal bar is joined to the neurocranium by three cartilage connections (see HOLMGREN, 1946). One lies caudal to the facial nerve, one between the facial nerve and the main part of the V_2-complex and one between the main part of the V_2-complex and a nerve forming the common origin of two palatinus trunks (see p. 338). These two palatinus trunks are not separated from the third palatinus trunk running to the nasal duct by any connection between the neurocranium and the dorsal longitudinal bar. It is true that the trabecle and the dorsal longitudinal bar intersect between the palatinus

trunk destined for the nasal duct and the other two palatinus trunks, but this intersection does not exist in Myxinid embryos. It is possible that r. palatinus in Myxine has no parallel in Petromyzon (p. 431). The exceptional position occupied by the palatinus nerve in relation to the other nerves of the V_2-complex is thus certainly obvious, but there seems to be no point in attempting to use this fact when discussing the metamerism of the head as long as our knowledge of the embryogeny of the Myxinids is incomplete. Having surveyed the questions concerning the metamerism in the prootic region, we shall now make a more detailed comparison between the trigeminus in Myxine and in Petromyzon.

1. THE BOUNDARIES BETWEEN THE TRIGEMINAL INNERVATION REGION AND THE REGIONS INNERVATED BY OTHER NERVES.

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The position of the bucco-pharyngeal plate in the embryo of Petromyzon corresponds to that of the velum in Ammocoetes. In Bdellostoma embryos the bucco-pharyngeal plate disappears without it being possible to trace in older embryos its former position. The velar musculature is innervated from the trigeminus both in the Myxinids and in the Petromyzonids. The posterior boundary of the mucous membrane innervated by the V_2-complex lies on the velum in both the Myxinids and Ammocoetes (or the corresponding structure in the adult Petromyzon). The velum in the Myxinids and the Petromyzonids are thus comparable structures. Further caudal the gut is innervated by n. facialis in Petromyzon but by n. glossopharyngeus in Myxine. N. facialis does not innervate the gut in Myxine. The hyomandibular and the two subsequent branchial pockets in Bdellostoma are reduced during the ontogenesis (see STOCKARD, 1906). If Myxine embryo undergoes the same process, which is probable, then the part of the pharynx belonging to the facial segment is partly or wholly suppressed during the ontogenesis of the Myxinids. This suppression and the migration backwards of the gills, which is described by DEAN (1899) and STOCKARD (1906), are two curious characteristics of the branchial region in the Myxinids. The connection between these two processes is perhaps not easily explained, as the rostral part of the pharynx is actually elongated in the Myxinids. A third characteristic of the Myxinids is that the region in the skin innervated by the V_2-complex consists merely of the immediate vicinity of the mouth opening and borders caudally on skin innervated by the most anterior spinal nerves. N. facialis does not take part in the innervation of the skin—at least not in Myxine. In Petromyzon the skin rostral to the most anterior branchial aperture persisting in the adult is innervated by cranial nerves. The boundaries between the innervation regions of the various cranial nerves lie almost longitudinally in Petromyzon. The regions are, from dorsal to ventral, a trigeminal, a facial and a glossopharyngeal.

2. N. OPHTHALMICUS.

It is doubtful whether n. ophthalmicus in the Cyclostomes actually has a lateralis component (cf. pp. 335 and 388). If such a component exists, then it joins the ophthalmicus in the Myxinids intracerebrally and in the Petromyzonids extracerebrally. According to ALLIS (1931 b), the fibres which pass from the facialis through the commissure to the ophthalmicus in Petromyzon are probably communis fibres. This hypothesis has the advantage of affording a new explanation of the nature of the commissure which has hitherto been assumed to carry lateralis fibres. There is, however, an objection to ALLIS's hypothesis; namely, it is difficult to envisage what purpose the communis fibres serve in the ophthalmicus of the Cyclostomes (cf. chp. XI). In the Petromyzonids the nasal capsule is innervated by a branch of the ophthalmicus. It is possible, but not established, that the nasal capsule in the Myxinids is also innervated by n. ophthalmicus. In contrast to the possible and the established differences between the ophthalmicus in the two groups of Cyclostomes, we have the following similarities: both have a peripheral extension in skin between the nasal capsule and the mouth opening, both are composed chiefly of general cutaneous fibres, and both develop as independent nerves, isolated from the rest of the trigeminus complex (for the ontogenesis cf. v. KUPFFER, 1893—1900, KOLTZOFF, 1902, DAMAS, 1944, and HOLMGREN, 1946). The similarities appear to confirm the homology between the ophthalmicus in the Myxinids and that in the Petromyzonids. It still remains to decide whether the nerve is an ophthalmicus superficialis or profundus. This question has given rise to much discussion (ALLIS, 1903, 1931 b, TRETJAKOFF, 1927 a). As Myxinids have no eye muscles the arguments must be based on the anatomy of Petromyzon. The relation between the ophthalmicus and n. trochlearis has not always been understood correctly. In Petromyzon the ophthalmicus runs ventral to n. trochlearis—a profundus characteristic—but dorsal to all the eye muscles—a superficialis characteristic. There are fish in which n. ophthalmicus superficialis is said to run ventral to n. trochlearis (cf. M. FÜRBRINGER, 1902). In view of the independent development of the nerve and its relation to n. trochlearis in Petromyzon, it appears, however, most correct to regard n. ophthalmicus in the Cyclostomes as an ophthalmicus profundus. According to ALLIS (1931 b) the course of n. ophthalmicus in the Cyclostomes dorsal to the branches of n. oculomotorius characterises it as a "portio ophthalmici profundi". According to the same writer (1925), a "portio ophthalmici profundi" ought to run dorsal to n. trochlearis, whereas "r. ophthalmicus profundus" ought to run ventral to n. trochlearis. ALLIS's interpretation does not therefore agree with the actual conditions in Petromyzon.

3. THE V_2-COMPLEX.

In the Myxinids the trigeminal nerves ending in muscles form a delimited unit. In Petromyzon the nerves from the dorsal and ventral spinal roots run to their terminal regions without forming common mixed nerves (cf. SCHNEIDER, 1879). In the rr. dorsales of the Myxinids the nerves coming from the dorsal spinal roots are also isolated from those coming from the ventral roots. On the other hand the rr. ventrales in the Myxinids are mixed nerves, formed by fibres both from the dorsal and ventral spinal roots (cf. RANSOM—D'ARCY THOMPSON, 1886). In Bdellostoma all nerves coming from the spinal roots in the tail region are, however, well isolated from one another and the spinal nerves in this region also have other characteristics in common with the spinal nerves of Amphioxus (cf. ALLEN, 1917. Cf. also p. 364 in the present paper). In order to be able to co-ordinate the facts discussed above, we must know whether the visceral motor component of the spinal nerves passes through the dorsal or ventral roots. According to FREUD (1878), the autonomic fibres ending in blood vessels pass through the dorsal roots in Petromyzon, but according to TRETJAKOFF (1927 a), autonomic fibres pass through the ventral roots to the alimentary canal in Petromyzon. As our knowledge of the courses of the visceral motor elements in the spinal roots of the Cyclostomes is so incomplete—nothing is known in the case of the Myxinids—we must confine ourselves to stating that the isolated courses of certain components in cranial and spinal nerves is probably an indication of a primitive organisation.

A. The Nerves and the Muscle Groups.

In the description given earlier on of the V_2-complex, an attempt was made to deal in the same section with nerves having the same main direction. The purpose of such a subdivision was to faciliate comparison between the present and earlier descriptions. The main direction is, however, a bad basis for subdivision.

A subdivision of the motor trigeminus in the Cyclostomes may be based on homologies of the innervated muscles. When SEWERTZOFF (1917) advanced the hypothesis mentioned on p. 426, he subdivided the trigeminus and facialis musculature in Petromyzon embryo into certain groups. These groups may of course exist, even if the conclusions which SEWERTZOFF drew are no longer valid. DAMAS (1944) criticizes the grouping made by SEWERTZOFF and states (p. 198): "Nous estimons que cette façon d'interpréter les ébauches musculaires buccales résulte d'une systématisation exagérée." As HOLMGREN (1946) found muscle groups in Myxine embryo comparable to those described by SEWERTZOFF in Petromyzon embryo, there is, however, every reason to ascer-

tain what bearing the subdivision of the musculature may have on the comparative anatomy of the motor trigeminal nerves of the Cyclostomes. In chapter IV in the present paper an analysis—in certain respects incomplete—was made of the development of the musculature in the Myxinids. TRETJAKOFF (1929 a) ascertained the connections between the muscle groups in Petromyzon embryo and the muscles of the Ammocoetes. A certain amount of criticism may, however, be directed against TRETJAKOFF's statements. M. buccalis posterior profundus in the embryo ought to correspond to "m. depressor labii superioris" (i.e. *le releveur de la lèvre postérieure* in DAMAS' nomenclature) since SEWERTZOFF states (pp. 93—94) that the muscle lies lateral to "arcus praebranchialis 3", i.e. the lateral mouth plate in 45-day old embryo. (SEWERTZOFF calls the muscle "le muscle buccal postérieur" on page 93, but it is clear from the context that he refers to m. buccalis posterior profundus.) No marked displacements should take place during the development from this 45-day stage to the youngest stages in the present material. "M. pharyngeus", i.e. DAMAS' *le muscle constricteur buccal* ought thus not to correspond to m. buccalis posterior profundus in the embryo but—judging from SEWERTZOFF's description on page 93—to m. constrictor velaris in the embryo. TRETJAKOFF states finally that all three velar muscles ("m. velocranialis", "m. velohyoideus" and "m. velothyroideus") correspond to "m. constrictor velaris profundus", but in actual fact mm. velares profundi in the embryo should be substituted for "m. constrictor velaris profundus".

HOLMGREN compares a buccalis group in Myxine embryo to m. buccalis posterior superficialis and profundus in Petromyzon embryo. The anterior buccalis group in Petromyzon embryo does not therefore have any corresponding structure in Myxinid embryos. This implies that r. muscularis anterior, apart from certain branches (see below), in the Myxinids corresponds to "r. basilaris" plus the branches innervating *le releveur de la lèvre postérieur* in Ammocoetes, whereas nerves corresponding to the remaining motor elements in "r. apicalis" of Ammocoetes are lacking in the Myxinids. ("R. apicalis" and "r. basilaris" are cited for reasons given on p. 405.)

HOLMGREN compares a velar group in Myxine embryo to m. constrictor velaris and mm. velares profundi in Petromyzon embryo, but as was pointed out on p. 328 of the present paper, probably not all the muscles in adult Myxine are represented in the embryonic stage described by HOLMGREN. Of the velar group, only the deeply seated m. craniovelaris and m. spinovelaris exist. Judging from their position in the velum, they should correspond to mm. velares profundi in Petromyzon embryo, which implies that rr. musculares velares in Myxine correspond to part of the motor component of r. mandibularis in Ammocoetes. Of the velar group in the Bdellostoma embryos described in chapter IV, there are to be found a superficial primordium of m. craniobasalis and primordia of m. flexor trabeculae and m. trabeculo-coronarius.

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The two latter muscles will not be discussed here. The position of m. cranio-basalis, which surrounds the buccal cavity, reminds one of the superficial position of *le muscle constricteur buccal* in the velar group of Ammocoetes. *Le muscle constricteur buccal* and all the other muscles in the velar group of Ammocoetes are innervated by branches of the ventrally directed r. mandibularis. M. cranio-basalis in Myxine is innervated by a nerve branch which issues together with the rostrally directed r. muscularis anterior but separates proximally from this nerve trunk. There are certainly more similarities between m. pharyngeus of adult Petromyzon and m. cranio-basalis in Myxine as m. pharyngeus is innervated by the rostrally directed r. subopticus, but even this comparison is doubtful as m. pharyngeus lies medial to r. subopticus whereas m. cranio-basalis lies mainly lateral to r. externus and r. muscularis anterior in Myxine. The question arises as to whether the homology between the muscle groups in the Myxinids and the Petromyzonids is invalid or whether the grouping of the nerve branches on main motor trunks is irrelevant for the homology of the nerve branches of the two Cyclostome groups. This question will be discussed further on pages 434 and 439. It should be pointed out that neither the connection between the embryonic muscle groups of Petromyzon and the muscles of Ammocoetes nor the connection between the embryonic muscle groups of the Myxinids and the muscles of adult Myxinids are fully established. The muscles of the piston mechanism and the facialis musculature were discussed on p. 413.

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B. R. palatinus.

In Myxine r. palatinus does not pass through the subocular fenestra. In Petromyzon all the branches from the V_2-complex pass through the subocular fenestra, apart from a very insignificant fibre bundle which can hardly be compared to r. palatinus. The question arises whether Petromyzon lacks a trigeminal branch corresponding to r. palatinus or whether it lacks the cartilaginous bars which in Myxine separate r. palatinus from the rest of the V_2-complex. These cartilaginous bars are the anterior connection between the trabecle and the dorsal longitudinal bar and the "palatine bar". (The "palatine bar" lies dorsal to the palatinus trunk destined for the dorso-medial wall of the buccal cavity but ventral to the palatinus trunk destined for the nasal duct.) If there exists in the V_2-complex of Petromyzon a nerve corresponding to the palatinus trunk running to the nasal duct in Myxine, then the relations between the skeleton and the trigeminal branches become very difficult to interpret in the Cyclostome group. However, Petromyzon has no nasal duct comparable to that of Myxine. The trunk of r. palatinus innervating the nasal duct in Myxine is thus probably missing in Petromyzon. A condition for the existence in the Petromyzon V_2-complex of nerves corresponding to the other palatinus trunks is that the anterior connection between the dorsal longitudinal bar and the

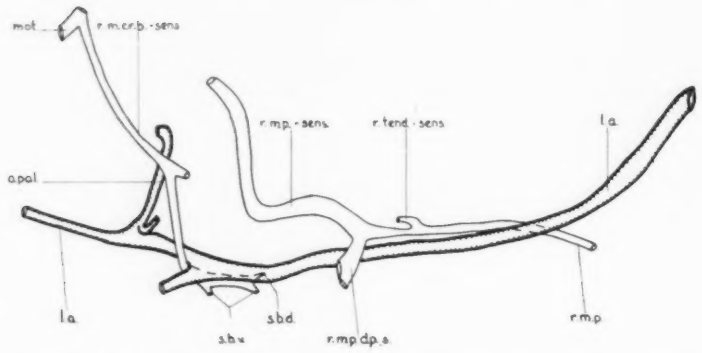

Fig. 46. Myxine, adult. Reconstruction of the lingual artery and some trigeminal nerves. Lateral view. 20 ×.

trabecle in Myxine has no corresponding structure in Petromyzon. This implies, however, that neither HOLMGREN's (1946, p. 31) nor JOHNELS's (1948, p. 264) interpretation of the subocular arch and adjacent cartilage in Cyclostomes is valid, and that the subocular fenestra in Myxine is not fully comparable to that in Petromyzon. The only remaining possibility is that a nerve homologous to r. palatinus is totally absent in Petromyzon, It is true that Petromyzon has no connection between the nasal capsule and the pharynx, but the animal has a long sac stretching from the nasal capsule down towards the pharynx and ending in a terminal vesicle. TRETJAKOFF (1926 a) states that changes in volume in this vesicle are due to changes in volume in the adjacent venous sinus and movements of m. postpharyngeus and m. pharyngeus and of the musculature of the gill basket. The vesicle may possibly affect the intake of water to the nasal capsule. It was not possible to observe any innervation of the sac and its terminal vesicle in the present material. In view of its possible function outlined above, it does not appear to be out of the question, theoretically, that the sac and its vesicle are not innervated apart from autonomic innervation. In Myxine the nasal duct and the naso-hypophysial duct offer free passage from the external nasal opening to the pharynx, and the need for innervation of this structure should be obvious. It may be pointed out that the innervation is extremely thorough in the regions of the Cyclostome head which in some way or other constitute a constricted passage for an incoming stream of water, *viz.* the vicinity of the mouth opening in both Myxine and Petromyzon, the surface of the velum facing the buccal cavity in Petromyzon and the posterior opening of the naso-hypophysial duct in Myxine. The velum in the Myxinids does not, on the other hand cause any marked constriction of the lumen of the digestive tract.

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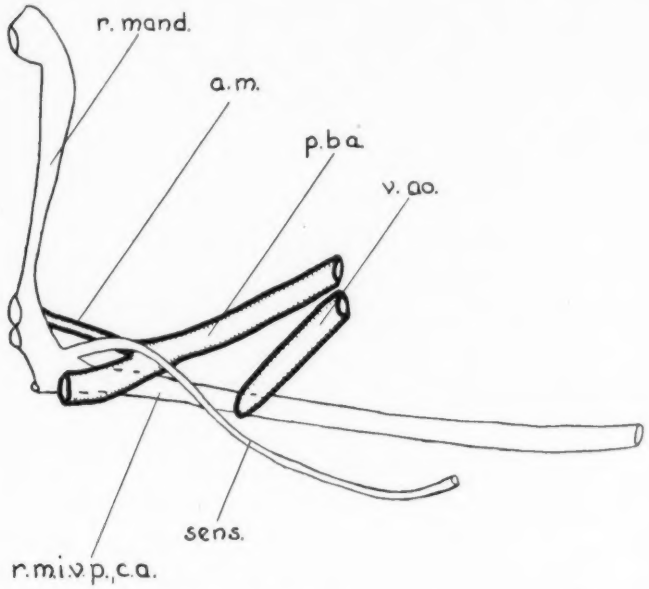

Fig. 47. Petromyzon, adult. Reconstruction of the main ventral arteries and r. mandibularis. Lateral view. 36 ×.

C. The Relation between certain Trigeminal Branches and Some Arteries.

There is, both in Myxine and Petromyzon, a trigeminal branch of uncertain character (pp. 345 and 377) running caudad close to the piston mechanism. The branches are either proprioceptive, visceral afferent (coming from blood vessels) or autonomic. In Myxine the nerve branch issues from the lateral part of the V_2-ganglion, joins r.m. cranio-basalis, separates from this nerve and passes lateral to the lingual artery (according to HOLMGREN'S nomenclature, 1946). Further distal it passes ventral to and finally medial to the artery (fig. 46). R. muscularis posterior in Myxine passes medial to the lingual artery. As far as it is possible to judge, the branch in question issues in Petromyzon from the medial part of the V_2-ganglion, joins r. mandibularis but separates from it further distally. The nerve branch passes lateral to "die parabranchiale Arterie" (TRETJAKOFF, 1927 b) in the vicinity of the point where this artery gives off "a. mandibularis" (TRETJAKOFF, l.c.). The terminal part of the ventral aorta turns laterad to the peribranchial space anterior to the first gill (TRETJAKOFF, p. 219). The nerve branch passes medial to the most terminal part of the ventral aorta (this part is not drawn in fig. 47). Further caudal it runs ventral to the ventral aorta. The caudally directed motor branch of r. mandibularis

passes medial to both the parabranchial artery and the terminal part of the ventral aorta. Further caudal it lies medio-ventral to the ventral aorta (cf. fig. 35).

No vessel corresponding to the terminal part of the ventral aorta in Petromyzon appears to exist in Myxine; no gill exists in this region in Myxine (cf. p. 363). The carotis ventralis in Ammocoetes (CORI, 1906) is transformed, according to TRETJAKOFF, into the parabranchial artery of the adult. The lingual artery constitutes the rostral continuation of the carotis ventralis in Ammocoetes and a vessel corresponding to the lingual artery exists according to TRETJAKOFF in the adult. Studies of Petromyzon specimens undergoing metamorphosis would probably be necessary before a definite decision could be arrived at on this point, but TRETJAKOFF's statement appears highly probable. Myxine has a lingual artery, homologous to the parabranchial artery and the lingual artery in Petromyzon (p. 419). No subdivision of the Myxine artery in a "parabranchial" and a "lingual" part can be realized. For the time being we ignore the subdivision of the artery in *both* Cyclostome groups and consider it as a single vessel. It runs lateral to r. muscularis posterior in Myxine and r. mandibularis in Petromyzon but medial to the autonomic (or visceral afferent or proprioceptive) trigeminal branch in both Myxine and Petromyzon. Should a homology actually exist between these vessels and nerves in Myxine and Petromyzon, three conclusions can be drawn. Firstly, it appears irrelevant whether the trigeminal branch from the ganglion emerges from the ganglion lateral or medial to the motor trigeminus (cf. p. 437). Secondly, r. m. craniobasalis must correspond to some part of r. mandibularis in Petromyzon, in spite of the fact that in Myxine the nerve originates as part of the rostrally directed r. muscularis anterior; this would, moreover, support the comparison made on page 431 between the muscle groups in Myxine and Petromyzon. Thirdly, there is reason to suspect that no structure exists in Myxine corresponding to the most anterior part of *m. infravélaire postérieur* in Petromyzon, since the trigeminal branch referred to in the beginning of the section runs lateral to the anterior part of the pharyngeal roll in Petromyzon but could not be traced as far caudal as m. tubulatus in Myxine.

D. The Morphogenesis of the V_2-Complex.

In the comparisons made hitherto between the V_2-complex in Myxine and Petromyzon, only some special problems have been dealt with. The V_2-complex will now be discussed as a whole. The motor trigeminus in the Cyclostomes consists proximally of an undivided powerful trunk coming from the motor root. The root has been defined by the writers who have studied the central nervous system. The motor trunk lies ventral to or embedded in the ventral part of the V_2-ganglion. Dorsal to the motor trunk, the sensory V_2-complex

divides into medial branches destined for the buccal cavity (in both Petromyzon and Myxine) and for the nasal duct and the naso-hypophysial duct (in Myxine), and lateral branches to the skin. Peripherally the sensory nerves retain their medial or lateral position. The medial branches are in Myxine, r. dentalis, rr. velobuccales and r. palatinus and in Petromyzon, r. velaris, r. suprapharyngeus (including some small somewhat similar branches), and the sensory branches of r. apicalis and r. mandibularis. (The sensory component of r. apicalis runs both in r. perforans and r. subpharyngeus.) The lateral branches constitute r. externus in Myxine. In Petromyzon the lateral branches consist of r. suborbitalis and r. cutaneus descendens together with a small bundle of fibres emerging direct from the V_2-ganglion. The motor trunk divides in Myxine into r. muscularis anterior, r. muscularis posterior and rr. musculares velares. In Petromyzon, the motor trunk is split up between r. apicalis, r. basilaris, r. mandibularis and some small motor branches given off proximally from the ramification point of the motor trunk. (R. apicalis and r. mandibularis are not exclusively motor.)

This comparison between Myxine and Petromyzon is based *inter alia* on the fact that the motor component is a completely or almost completely isolated unit. In order to test the validity of the comparison we shall first discuss the embryonic development of the Cyclostomes. Unfortunately, the Bdellostoma embryos in the present material can contribute few data of any interest here, as the staining does not allow of the necessary analyses of the nerves. The only possible contribution is a negative one, namely the fact that the rr. velobuccales are in stage I joined proximally to r. muscularis posterior but in stage II to r. dentalis instead. This may be taken as indicating that the separation of the motor component from the sensory component is effectuated during the embryonic development and has no fundamental significance. The different courses of rr. velobuccales in the two stages may, however, also be the result of displacements caused by the growth—displacements which have no bearing on the present discussion. The literature dealing with the embryonic development offers few data of interest here. v. KUPFFER (1893—1900) writes that the motor root sends off a nerve which joins the sensory "mandibularis" nerve in stages E VIII and E IX—the oldest Bdellostoma embryos he describes. Whether the sensory "maxillaris" nerve also receives a contribution from the motor root he is unable to decide. (By the sensory "mandibularis" nerve v. KUPFFER presumably means r. dentalis and rr. velobuccalis and by the sensory "maxillaris" nerve, the r. externus-r. palatinus complex.) It is difficult to discuss NEUMAYER's work (1938) since he has, for example, misunderstood "r. maxillaris posterior" in Bdellostoma (nomenclature taken from WORTHINGTON, 1906). Fig. 14 in WORTHINGTON's work has presumably proved misleading, because the nerve in question was incorrectly drawn in this figure as one of the most lateral nerves, whereas in actual fact it is a branch of r.

palatinus. HOLMGREN states regarding a Myxine embryo (1946, p. 56): "The motor trigeminal issues separately behind the mandibular ganglion". v. KUPFFER (1893—1900) has given a detailed description of the embryonic development of the trigeminus in Petromyzon. He appeares to be more doubtful about the course of the motor and sensory fibres in Petromyzon than he is when describing the ontogenesis of Bdellostoma. This is quite natural as the motor and sensory elements in the trigeminus of adult Petromyzon are far less well separated than the corresponding elements in the adult Myxinids. v. KUPFFER (l.c. part 3, p. 39) says, however, that the motor fibres in the younger stages run scattered through the V_2-ganglion whereas in an older stage they are combined into a single group. The possibility of making such an observation without access to material with impregnated nerve fibres appears to be limited.

The following arguments based on the anatomy of the adult Cyclostomes can also be advanced against the comparison made between the trigeminus in Myxine and Petromyzon.

1. Certain writers having studied the medulla oblongata in Petromyzon state that the roots which in the present work are regarded as motor also contain a sensory component. The writers, however, whose interpretation of the abducens root agrees with the observations made on the present material, doubt the existence of any such sensory elements.

2. The motor root in Myxine is well delimited from the V_2-ganglion. In Petromyzon this is not the case, and the possibility of an exchange of fibres between the motor root and the V_2-ganglion cannot be entirely ruled out. Figs. 8 and 23 should give an idea of the difference.

3. With few exceptions, the motor branches of the trigeminus in Myxine are well isolated in their peripheral courses from the branches emerging from the V_2-ganglia. In Petromyzon this is not the case. In the distal part of r. apicalis it is particularly difficult to separate the motor and sensory components in adult. Proximally in r. apicalis the sensory component lies medial to the motor one, but it is conceivable that the relations between the components change before the peripheral branches are sent off to their respective innervation regions. In Ammocoetes it is easier to observe the distribution of the sensory and motor components in the distal part of "r. apicalis" than in the proximal part of r. subopticus and in r. mandibularis.

4. In one adult Petromyzon specimen and in one Ammocoetes specimen certain nerve branches have an aberrant course (pp. 374 and 378) which contradicts the comparison between Myxine and Petromyzon set forth above. In both cases the aberrant course occurs only in one half of the body. Nerve branches with aberrant courses are by no means rare in the Cyclostomes (cf. chapter VIII).

5. There is reason to suspect that certain trigeminal branches consist of fibres that are proprioceptive or visceral sensory or belong to the autonomic system. They are those entering the tendon of m. clavatus in Myxine and the

tendon of m. cardio-apicalis in Petromyzon and the fine fibres accompanying r.m. cranio-basalis in Myxine and the finely calibred bundle running caudad alongside *m. infravélaire postérieur* in Petromyzon. These branches could not be made to fit into the suggested schema for the V_2-complex. This fact is perhaps symptomatic. No schema comparable to that of the V_2-complex can be applied to the more caudally situated cranial nerves, all of which differ in composition from the trigeminus. The reason why the sensory and motor elements in the posterior cranial nerves cannot be separated during their peripheral course is perhaps partly the fact that the components are more closely packed in the nerves and partly that the calibre of the fibres is unsuitable for such a separation. Of greater importance here is HOLMGREN's (1919) and JANSEN's (1930) statement that the roots of the vagus group are mixed in Myxine and JOHNSTON's (1902, 1905) and ADDENS's (1933) statement that it is not possible to separate the motor and sensory fibres in the vagus of Petromyzon at the point where it emerges from the brain. Visceral sensory and autonomic fibres play an important rôle in the facial, glossopharyngeal and vagus nerves. It is not unlikely that the schema of the V_2-complex is conditioned by the fact that the nerve is mainly composed of a general cutaneous and a special visceral motor component.

6. Some of the proprioceptive fibres discussed under point 5 may possibly innervate sense organs for registering tension in muscles. STEFANELLI (1932) certainly describes sensory nerve terminations in the trigeminal musculature in Petromyzon. ALLEN (1917) describes muscle spindles in m. cordis caudalis in Bdellostoma. No sense organs registering tension in the trigeminal musculature of the Myxinids have been described, probably because no suitable methods have been used. The central connections of the possibly proprioceptive fibres in the trigeminus and the facialis are discussed on pages 360 and 422. It should appear from this discussion that practically nothing is known of the central connections. Of the peripheral course of fibres coming from sense organs in the trigeminal musculature we only know that the fibres probably accompany the motor fibres from the muscles.

FUSARI (1907 a) describes the innervation of granular cells in the epithelium of Ammocoetes. From what nerve trunks these cells are innervated is, however, unknown. For the time being the possibility cannot be abandoned that the skin branches of the trigeminus may contain autonomic fibres, innervating granular cells.

From the discussion in point 6 it is obvious that the terms "motor" and "sensory" trigeminal branches used hitherto in the present paper may be misleading as the "motor" branches may contain sensory fibres from sense organs registering the tension in the muscles and as the "sensory" branches may contain motor fibres for gland cells. The expressions "nerves destined for the muscles, for the skin and for mucous membrane" are better and will be used subsequently.

7. In the oral hood of Ammocoetes and in the suctorial disc of adult Petromyzon we find the boundary between the innervation regions of r. suborbitalis, and r. apicalis, i.e. the boundary between the lateral and medial V_2-branches destined for skin and mucous membrane. The exact position of the boundary has not been ascertained on the present material, but the approximate position should be clear from the descriptive part of this paper. N. ophthalmicus too innervates part of the oral hood and the suctorial disc. In addition this nerve innervates skin on the dorsal side of the animal. In Myxine the mouth opening constitutes a boundary between skin innervated by r. externus and mucous membrane innervated by r. palatinus and r. dentalis. In this animal n. ophthalmicus, moreover, innervates skin rostro-dorsal to the mouth opening, i.e. in the vicinity of the nasal opening. The agreement between Petromyzon and Myxine thus seems fairly good but it is partly imaginary. The author has tried to establish on page 431 that Petromyzon probably lacks a homologue to r. palatinus. This deficiency in the agreement should imply that certain medial areas in the cranial and visceral surfaces, constituting the anterior boundary of the embryo (cf. ALLIS, 1924 a, 1931 a, 1938), develop into far less extended regions in adult Petromyzon than they do in adult Myxine (cf. pp. 353—354). Finally, there is an exception to the above description of the innervation of the vicinity of the mouth opening in Myxine. One branch from r. externus runs in the floor of the buccal cavity towards the dental plate. This exception is not in any way surprising. On the contrary, one might well ask if the boundary between the lateral and medial branches destined for the skin and the mucous membrane respectively has any value for comparisons within the Cyclostome group. Both the medial and the lateral branches contain, of course, general cutaneous fibres, but no visceral sensory fibres. The buccal cavity develops as an ectodermal invagination. The innervation region of r. externus is restricted to the skin in the vicinity of the mouth opening in Myxine whereas the trigeminal innervation region in the skin of Petromyzon stretches between the border of the suctorial disc and the first external branchial aperture. The possibility that trigeminal fibres are displaced between the lateral and medial branches destined for the skin and the mucous membrane during the phylogenesis of the Cyclostomes cannot be entirely ruled out. Such a displacement would then correspond to a more or less far reaching invagination of the ectoderm into the stomodaeum and, in connection therewith, a displacement of the position of the mouth opening in the ectoderm. The trigeminal trunks running to muscles should constitute an obstacle for such a displacement of nerve fibres so that the displacement must take place dorsal and rostral to the trunks destined for the muscles.

In the above seven points some reservations were advanced—and to some extent dismissed—against the comparison between the V_2-complex of Myxine and Petromyzon set forth on page 434. The comparison is modified but the

reservations nevertheless do not invalidate it. No examinations of the central trigeminal connections or of the trigeminal end organs have been carried out on the present material. The comparison is based on the correspondence between the courses of the V_2-branches in the root and ganglion region on the one hand and the peripheral distribution of the branches between muscles, skin and mucous membrane on the other.

An attempt to subdivide the V_2-complex into maxillar branches and mandibular branches has been made on pp. 354 and 384. It should be clear from these attempts that such a subdivision is uncertain and must be incomplete. JOHNSTON (1905, 1908 a) and CORDS (1929 a) have already questioned the justness of subdividing the V_2-complex of the Cyclostomes into maxillar and mandibular branches. JOHNSTON points out that the "maxillaris" innervates the floor of the buccal cavity in Petromyzon by means of r. subpharyngeus. The region ought to be innervated by the mandibularis. The fan-like distribution of the motor trigeminal branches and the existence of motor elements in the rostrally directed branches caused CORDS to doubt whether a subdivision into maxillar and mandibular branches could be applied to the Cyclostomes. According to STENSIÖ (1927, 1932), the Cyclostomes are primary agnathous. JOHNSTON'S, CORD'S and STENSIÖ'S data appear to constitute good reason for not subdividing the V_2-complex into maxillar and mandibular branches. As was mentioned on page 354, there are, however, some similarities between the internal mandibular skeletal arch of Myxine and that of the Gnathostomes according to HOLMGREN (1942 a, 1946), and on the next page it was stated that a subdivision into maxillar and mandibular branches may be justified even if the similarities in the skeleton should not exist. There may thus be in the Cyclostomes a trace of the subdivision which is only fully established in the Gnathostomes.

A subdivision of the trigeminal branches destined for the muscles, based on the presumed homologies between the embryonic muscle groups, is attempted on page 429. (It is by no means certain whether the homologies of the embryonic muscle groups are of any significance when the Cyclostomes are compared with the other Chordates.) This subdivision cannot be carried out if any importance is attached to the main direction of the nerve branches destined for muscles (p. 431). From the comparisons of the muscles and nerves of the piston mechanism given on p. 413, it should also be clear that the main directions of the V_2-branches are of no importance for the comparative anatomy of the Cyclostomes.

As regards the medial branches to mucous membranes, the author has presumed that Petromyzon lacks the homologue of r. palatinus. Only surmises can be made as to whether the homologue of rr. velobuccales and r. dentalis in Myxine is to be found in r. apicalis and r. mandibularis in Petromyzon. An indication of homology is the fact that both r. dentalis and r. subpharyngeus

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rami apicalis innervate the mucous membrane on the movable terminal part of the piston mechanism, which part is for other reasons (p. 413) interpreted as a homologous structure within the Cyclostome group. This comparison, too, is possible only if no importance is attached to the main directions of the V_2-nerves.

Most stress should be laid upon the difference between, on the one hand, the branches of the V_2-complex destined for the muscles and, on the other, those destined for the skin or the mucous membrane. Probably in connection with the progressive development of the mandibular segment during the phylogenesis of the Cyclostomes the trigeminal nerves destined for the muscles are arranged like a vertical fan. Branches to the skin and the mucous membrane which at early phylogenetic stages appear to have lain chiefly rostral to the muscle nerves, have become medial and lateral to the muscle nerves as a result of the progressive development of the mandibular segment.

XIII. THE TRIGEMINUS AND THE CRANIAL SKELETON.

If the ontogenesis reflects at all the presumed displacement of the branches to the skin and mucous membrane discussed on page 438, then the displacement must take place at a very early stage in the embryonic development. It may be of interest, however, to discuss to what extent there is in the adult a "path of the displacement" where skeletal elements are avoided. In Myxine it is easiest to imagine the displacement between the dorsal group of skeletal elements consisting of the subnasal cartilage, the tentacle cartilage II and the cornual cartilage and the ventral group consisting of the basal plates and the labial cartilage with the tentacle cartilages I and III. In Petromyzon, the most likely "path" appears to be between the dorsal group formed by the anterior and posterior dorsal plates and the posterior lateral plate and the ventral group formed by the cartilages of the piston mechanism and the anterior lateral plate. The lateral mouth plate in Ammocoetes need not be considered, as most of the rostrally directed branches of the trigeminus run lateral to this skeletal element. If we imagine that the displacement takes place along the paths outlined above, then only the annular cartilage in Petromyzon and a ligament between the labial and cornual cartilages in Myxine lie in the way. The ligament is said to contain cartilage in Bdellostoma (AYERS, 1931).

The above is an attempt to test the comparison between the trigeminus in Myxine and Petromyzon from all points of view. The discussion may appear far too speculative, but recent studies of the skeleton of the Cyclostomes provide a concrete basis for the argument. HOLMGREN (1946) and JOHNELS (1948) compare the labial cartilage in Myxine to the anterior lateral plate in Petromyzon, and JOHNELS supports the comparison by showing that the anterior lateral plate develops during the metamorphosis in connection with the apical

cartilages and the piston cartilage. JOHNELS compares the cornual cartilage in Myxine to the posterior lateral plate plus the anterior dorsal plate in Petromyzon, and certain of the stages of the metamorphosis he describes support this homology very convincingly.

HOLMGREN's and JOHNELS's arguments regarding the relations between the trigeminus and the skeletal elements are, however, open to criticism. They point out that a V_2-branch runs medial to the cornual cartilage or the posterior lateral plate plus the anterior dorsal plate, respectively. The same branch is said to run lateral to the labial cartilage or the anterior lateral plate, respectively. The writers must refer to r. externus in Myxine and r. apicalis in Petromyzon (the latter nerve has such a course in certain stages of the metamorphosis, see p. 405). R. externus is a lateral branch to the skin, whereas r. apicalis is a medial branch destined for muscles and the mucous membrane of the buccal cavity and the suctorial disc. It appears more adequate to compare the course of r. externus in Myxine to that of r. suborbitalis in Petromyzon. These nerves run lateral to the labial cartilage or the anterior lateral plate, respectively. R. suborbitalis runs ventral to the subocular arch out to the subcutis in Petromyzon. If instead it ran out to the subcutis somewhat more rostrally, then it would pass ventral or medial to the connection between the subocular arch and the posterior lateral plate and ventral or medial to the posterior lateral plate itself. If we wish to homologize the relation between r. suborbitalis and the posterior lateral plate plus the anterior dorsal plate in Petromyzon with the relation between r. externus and the cornual cartilage in Myxine, such an imaginary displacement is, however, by no means necessary. The only branch of r. externus which, in the youngest of the Bdellostoma embryos described in the present paper, has any close connection with the cornual cartilage, runs caudal to the cartilage. In adult Myxine r. externus runs mainly ventral to the cornual cartilage.

If a homology exists between individual motor nerves in this region in Myxine and in Petromyzon, then, as was stated on page 430, it is between r. muscularis anterior in Myxine and "r. basilaris" plus the branch to *le releveur de la lèvre postérieure* in Ammocoetes. Judging from JOHNELS's description, r. basilaris probably runs lateral to the primordium of the anterior lateral plate during the metamorphosis of Ammocoetes. In Myxine, r. muscularis anterior runs medial to the labial cartilage. The parts of the muscle nerves lying in this region may be interpreted as terminal branches. Too much weight should not be attached to the relation between the skeleton and the terminal branches destined for the individual muscles, because it is only the embryonic *groups* of muscles which can be homologized, whereas it is pointless to try to make comparisons between the single muscles in Myxine and Petromyzon. It is, of course, more than probable that different muscle individuals are preserved in Myxine and Petromyzon during the phylogenetic development of the Cyclostome group.

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XIV. THE LATERALIS ANTERIOR.

It is doubtful whether the trigeminus carries any lateralis fibres in Myxine and Petromyzon (chp. V:2 and VI:2). In Bdellostoma, r. externus or n. ophthalmicus (possibly both) carry lateralis fibres. A n. buccalis (r. buccalis) exists in both the Myxinids and the Petromyzonids. N. buccalis in the Myxinids has two special characteristics: the nerve is entirely independent of n. facialis and contains, in addition to a lateralis component, a general cutaneous component. A lateralis component exists in the main trunk of the facialis in the Petromyzonids and possibly also in the Myxinids (p. 360). R. recurrens facialis is only to be found in the Petromyzonids. The most curious characteristic of the lateralis anterior in the Cyclostomes is that the existence of a r. ophthalmicus superficialis facialis is badly documented. This calls for further studies.

A pineal (suprapineal) line has been described in a number of extinct groups of fish (Stensiö, 1927, 1932, Holmgren, 1942 b) and in certain embryonic stages of Protopterus (Pehrson, 1949). The innervation of the neuromasts in the pineal line of these groups of fish does not appear to have been established. The homologies are based on the topographical position of the pineal line and the general pattern of the neuromast system. The present writer only wishes to point out here that the pineal line in Petromyzon is innervated from the glossopharyngeus. The bearing of this fact on the interpretations of the head lines of pits ought to be discussed.

XV. THE AUTONOMIC SYSTEM.

Razzauti (1917) deals in detail with the literature on the autonomic system in Petromyzon and discusses the relevant problems. In the following, the account of the literature is incomplete.

1. PERIPHERAL CELL BODIES OF SPINAL GANGLION CELL TYPE.

The existence of such cell bodies in rr. dorsales and rr. ventrales of the spinal nerves of the Myxinids was dealt with on page 364. Langerhans (1876) and Freud (1878) describe peripheral cell bodies in corresponding nerves in Petromyzon. Freud states that some are of the same type as the cell bodies in the spinal ganglia while others have an aberrant appearance. Freud's description gives the impression that the peripheral cell bodies are at least partly cell bodies which have migrated from the spinal ganglia along the nerves. He investigated mainly the tail region in Petromyzon. It is in the

tail region of Bdellostoma that peripheral cell bodies are most abundant (ALLEN, 1917). The present writer inclines to ALLEN's interpretation of the peripheral cell bodies in the spinal nerves of the Myxinids, namely, that their position must be regarded chiefly as an expression of the diffuse arrangement of the spinal ganglia, recalling the arrangement in Amphioxus. The same interpretation may presumably be applied to the conditions in Petromyzon. RAZZAUTI does not appear to have seen the peripheral cell bodies which, according to FREUD, have the same structure as cell bodies in the main part of the spinal ganglia, since he regards all peripheral cell bodies as "sympathetic" (autonomic) and denies that any peripheral cell bodies have migrated from the spinal ganglia. Further investigations will be necessary to decide whether the cell bodies of spinal ganglion cell type really are autonomic or not.

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2. N. VAGUS.

MÜLLER (1839) considers that the autonomic system in the Cyclostomes consists solely of n. vagus. In the Myxinids, n. vagus follows the digestive tract even caudal to the branchial region. In the Petromyzonids, the nerve changes behind the branchial region into a diffuse plexus in the digestive tract with scattered cell bodies (cf. TRETJAKOFF, 1927 a).

3. THE SYMPATHETIC TRUNK.

Several writers are agreed that there is in the spinal region of the Cyclostomes no sympathetic trunk formed by ganglia and nerve trunks running between them. On the other hand, MARCUS (1910)—Myxine—and JULIN (1887) and KRAUSE (1923)—Petromyzon—describe ganglia situated near the large dorsal vessels and connected to the spinal cord. The ganglia are said to lack longitudinal connections. The existence of a "sympathetic trunk" of this incomplete type has, however, also been denied (BRANDT, 1922, GIACOMINI, 1902). Even if the presence of such ganglia is open to doubt, there certainly exist autonomic or visceral sensory branches from the spinal nerves. These branches are directed toward the blood vessels and the digestive tract. FREUD (1878), DOHRN (1886, 1888), KRAUSE (1923) and TRETJAKOFF (1927 a) describe such branches in Petromyzon and on page 365 in the present paper such branches are described in Myxine. DOHRN's and TRETJAKOFF's statements refer to branches which reach the caudal part of the gut. KRAUSE states that in general the autonomic branches reach the gut via blood vessels. WHITING (1948) describes conditions in a unique material, i.e. young Ammocoetes specimens between 7 and 10 mm long, stained with specific nerve stain. He writes (p. 376): "Evidently the viscero-motor component of the spinal nerves,

so far as it exists at this stage, can be concerned only with the innervation of blood-vessels, and perhaps of the anal region of the gut (DOHRN, 1888)".

In connection with the occurence of autonomic branches from the spinal nerves, it is appropriate to quote FÄNGE (1948): "Concerning the pharmacological reactions of the intestine of Myxine, no peculiarities were observed, which might be explained by the primitive nature of visceral innervation in this animal" (i.e. the fact that the visceral innervation is said to be supplied solely by n. vagus).

4. PERIPHERAL CELL BODIES DIFFERING FROM SPINAL GANGLION CELLS.

Such cell bodies have been described in many parts of Petromyzon. On the basis of their appearance and situation, the cells have been presumed to be autonomic in character; an assumption which is more justified than in the case of the peripheral cell bodies discussed earlier on. No such autonomic cell bodies were observed in the present material either in Myxine or in Petromyzon. As, however, it might be possible to observe them using another method, the present writer refrains from expressing any opinion on them. The reader is refered to the following literature: TRETJAKOFF, 1927 a, various places throughout the entire animal; JOHNSTON, 1908 a, various places in the rostral parts of the animal; JULIN, 1887, the gut; FREUD, 1878, and FUSARI, 1907 b, blood vessels; FUSARI, 1907 a, and RAZZAUTI, 1917, the subcutis; FUSARI, 1907 b, mucous membrane of the branchial part of the gut.

5. AUTONOMIC AND VISCERAL AFFERENT BRANCHES OF THE TRIGEMINUS AND THE FACIALIS.

JOHNSTON has made one of the most important contributions to our knowledge of the autonomic nervous system in the Cyclostomes. He writes (1908 a, p. 599): "... a large system of fibers makes its exit from the brain with the VII nerve which functions in connection with the control of the circulation at least in the branchial region. Whether fibers join this from other nerve roots still remains questionable ..." This quotation refers to adult Petromyzon but agrees well with FUSARI's statement (1907 b) that the vessels in the branchial region are richly supplied with nerve plexa and "sympathetic" cell bodies in Ammocoetes. The nerves which, according to JOHNSTON, belong to the autonomic (and visceral sensory?) system are r. sympathico-branchialis and that which above is referred to as the ventral branchial nerve bundle of r. hyomandibularis, and these nerves are found both in the adult and in Ammocoetes. In the present paper, certain facialis fibres in Myxine have been interpreted as probably proprioceptive or possibly visceral afferent (coming from blood ves-

sels, p. 360). Moreover, both in Petromyzon and in Myxine a trigeminal branch has been described which may be autonomic or visceral afferent (coming from blood vessels) or proprioceptive. If the autonomic character of these nerve branches can be established, then the Cyclostomes possess a system of autonomic branches from the cranial nerves, which lies ventral to the digestive tract. Such a system is, as far as is known, totally lacking in the Gnathostomes.

XVI. THE CYCLOSTOMES AND THE CEPHALASPIDS.

Most of our knowledge of the prehistory of the Cyclostomes is derived from STENSIÖ's work (1927, 1932). He pointed out the great similarities between Petromyzon and the Cephalaspids. Among these similarities may be mentioned the existence, in both forms, of a "hypophysial sac", connected with the nasal capsule, the existence of only two semicircular canals, the sac-form of the gills and the extension of the cranial skeleton. The last-mentioned similarity has been further analysed by HOLMGREN—STENSIÖ (1936), DAMAS (1944) and JOHNELS (1948). The last two authors in particular advanced somewhat modified views on the comparison of the cranial skeleton in Petromyzon and the Cephalaspids.

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From STENSIÖ's works it also appears that there are important differences between the Cephalaspids and Petromyzon. Among these differences should be mentioned the fact that the entire gill region is far more rostrally situated in the Cephalaspids than in the Cyclostomes, that the mandibular segment has about the same dimensions as the other cranial segments in the Cephalaspids whereas in the Cyclostomes it is far larger than the other cranial segments. Finally, the praemandibular segment is a complete segment and the ophthalmicus a complete branchial nerve in the Cephalaspids in contrast to the character of the praemandibular segment and ophthalmic nerve in all recent Craniotes (cf. however the discussion below).

STENSIÖ's interpretation of the cranial nerves in the Cephalaspids has not remained uncontradicted. An account will be given of ALLIS's views (1931 b). ALLIS considers that the nerves V_1 and V_2 (STENSIÖ's nomenclature) distal to the orbit are actually r. maxillaris and r. mandibularis of the V_2-complex. This interpretation implies that the ophthalmicus must be searched for in some other part of the head of the Cephalaspids. The most probable solution is then that n. ophthalmicus passed through the orbit to the skin. If this is the case its position cannot be ascertained in fossil material. According to this reinterpretation of the nerves n. ophthalmicus runs dorsal to the facial artery as is the case in Ammocoetes. According to STENSIÖ's interpretation the nerve runs ventral to the artery in the Cephalaspids. According to ALLIS, the praemandibular segment in the Cephalaspids is rather incomplete. However, the

similarity between "the praemandibular ridge" with its nerve and artery and the subsequent branchial ridges, aortic arches and branchial nerves is so obvious from STENSIÖ's description that we can hardly deny that "the praemandibular ridge" and the pertaining structures is an almost complete branchial segment. ALLIS does not deny that "the praemandibular ridge" in the Cephalaspids is of praemandibular origin but he considers—for reasons which will not be gone into here—that "the praemandibular ridge" is no serial homologue "of the visceral bars developed in the walls of the alimentary canal".

There still remain some unsolved problems, even if we accept ALLIS's interpretation of the trigeminus in the Cephalaspids. Vena capitis lateralis in Ammocoetes is distributed mainly in the brain, but in the Cephalaspids the vein is also distributed in a considerable region rostral to the brain. The nerve section, denoted l by STENSIÖ (for instance fig. 28, 1927), is said to carry lateralis fibres to the ophthalmicus. HOLMGREN (1942 b) points out, however, that no supraorbital line exists in the lateralis-system of the Cephalaspids (cf. p. 442 in the present paper).

An attempt will now be made to re-interpret the blood vessels and nerves in the head of the Cephalaspids. CORI (1906, pp. 48 and 54) and HATTA (1923, p. 182) describe how in early Ammocoetes stages v. facialis runs into vena capitis lateralis by way of a vein passing between the trigeminal and the facial ganglion. In later Ammocoetes stages v. facialis runs straight into carotis anterior. This alteration of the venous system has been confirmed by DANIEL's studies (1935) of living Ammocoetes. V. facialis and its branches are distributed over a considerable part of the head of Ammocoetes rostral to the brain. The vein may be homologous to the part of vena capitis lateralis which, according to STENSIÖ, runs rostral to the orbit in the Cephalaspids. The real rostral continuation of vena capitis lateralis would then run within the brain in the Cephalaspids. The junction of vena facialis and the real rostral continuation of vena capitis lateralis would then lie within the orbit. The proximal part of vena facialis should then run between the trigeminus and the facialis as in CORI's and HATTA's statements regarding young Ammocoetes. Such a course corresponds better to an interpretation of the cranial nerves in the Cephalaspids differing from STENSIÖ's. This new interpretation implies on the whole that the designations of some cranial nerves are displaced one step craniad. Starting from fig. 28 in STENSIÖ's work (1927) the ophthalmicus would run proximally in nerve V but distally it would pass through the orbit to the skin. The rest of the trigeminal nerves would run in nerve V and pass to V_1 in STENSIÖ's restoration. The facialis would correspond to l and V_2 and send out the buccalis (bu). N. glossopharyngeus would pass from the root VIIIp. to VII, whereas the vagus would correspond to IX + X. With this re-interpretation, the praemandibular segment and n. ophthalmicus in the Cephalaspids would not differ from the praemandibular segment and the ophthalmicus in recent

Craniotes. The new interpretation of the nerve section 1 is easier to accept than STENSIÖ's in view of our present knowledge of the lateralis system in the Cyclostomes. In the re-interpretation, n. facialis would pass through the orbit (only for a short distance in Kieraspis) and n. glossopharyngeus and n. vagus would pass through the labyrinth cavity. Thi situation can be said to lessen the value of the hypothesis. As was pointed out above, the branchial region in the Cephalaspids is, however, far more rostral than that in Petromyzon and it is moreover impossible to compare in detail the orbit and the labyrinth cavity in the Cephalaspids to the orbit and labyrinth cavity in Petromyzon. The orbit in Petromyzon is far less well delimited than that of the Cephalaspids, and the labyrinth cavity of the Cephalaspids differs from that of Petromyzon as the large electrical nerves pass through the labyrinth cavity of the Cephalaspids.

This discussion concerns a topic on which the author is by no means an expert and the re-interpretation made above must be regarded as a hypothesis. Should it nevertheless prove to be correct, it would imply that the differences between the ophthalmicus and the praemandibular segment in Cephalaspids and those in Cyclostomes are considerably reduced.

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XVII. SUMMARY.

1. The mutual relations between certain nerve branches and the relations between certain nerve branches and other structures are subjects to an intraspecific variation within the Cyclostomes. The question as to what is norm and what is deviation could not be treated statistically.

2. Two embryonic stages of Bdellostoma are described. The stages illustrate the development of the trigeminus and facialis musculature and the prootic cranial nerves of the Myxinids.

3. N. trigeminus, n. buccalis and n. facialis and some other nerves in the head of adult Myxine are described. Summaries of the courses of the trigeminal branches are found on pages 334, 341 and 351. A comparison with the two Bdellostoma embryos and a study of the literature concerning adult Bdellostoma indicate a far reaching similarity between the peripheral courses of the cranial nerves in Myxine and Bdellostoma.

4. N. trigeminus, n. facialis, the eye muscle nerves and some other nerves in the head of Ammocoetes and adult Petromyzon are described. A summary of the course of the trigeminus and the facialis can be found on page 403 under the heading "Ammocoetes and the adult Petromyzon". By means of the facts set forth in this investigation, a detailed comparison can be made between the peripheral courses of the sensory trigeminal branches and n. facialis in Ammocoetes and those in the adult.

5. R. palatinus occupies a unique position in n. trigeminus of the

Myxinids. The distribution of r. palatinus in adult Myxine fits in well with the data known on the ontogenesis of the nasal duct, the nasal capsule and the naso-hypophysial duct in the Myxinids. There are two mixed nerves in the trigeminus of Myxine. In both instances the components can be separated by means of the calibre of the fibres. Apart from this the nerves destined for muscles in Myxine run isolated from nerves destined for the skin and the mucous membranes.

As to the trigeminus of Petromyzon, it should be mentioned that *m. constricteur buccal* in Ammocoetes is innervated by r. mandibularis, that r. velaris and r. suprapharyngeus in the adult are sensory nerves and that a r. recurrens rami apicalis exists both in Ammocoetes and the adult and that m. copuloglossus obliquus is innervated by r. basilaris in the adult.

The relations between r. mandibularis and the parabranchial artery in Petromyzon is compared to the relations between the two mixed trigeminal branches and the lingual artery in Myxine.

6. N. facialis in Myxine has two ganglia, varying somewhat in character. Fine calibre VII fibres, either proprioceptive or visceral afferent (coming from blood vessels) exist in Myxine. The need for new investigations of the peripheral endings of these fibres and of the facial nuclei in the medulla is stressed.

Apart from r. sympathico-branchialis, there exist in Ammocoetes and adult Petromyzon two long branchial facialis nerve bundles. N. facialis innervates both *m. infravélaire inférieur* and *m. vélaribranchial* in the adult.

7. The small rostral root (roots) in the motor trigeminus complex does not belong to n. trochlearis but to n. trigeminus. N. abducens can be traced through the root complex to a descending root bundle in the medulla.

8. The term "spino-occipital" for the most anterior spinal nerves should be abolished in the Cyclostomes.

9. The existence of an independant buccalis nerve in the lateralis system of the Myxinids is confirmed. The pineal line in Petromyzon is innervated by r. postorbitalis IX. Both n. glossopharyngeus and n. vagus probably carry a component originating in the lateralis posterior in Petromyzon.

10. The proprioceptive system in the head of the Cyclostomes is on the whole unknown. A branch entering the tendon of m. clavatus in Myxine and that of m. cardio-apicalis in Petromyzon and some other trigeminal and facialis branches in the Cyclostomes may possibly consist of proprioceptive fibres. (The system is discussed on pages 360, 422, 436—437.)

11. Some of the above-mentioned presumably proprioceptive fibres may possibly be visceral afferent or autonomic instead. In agreement with JOHNSTON's statement, r. sympathico-branchialis and the ventral branchial hyomandibularis nerve bundle in all probability carry autonomic fibres. Visceral branches from the most anterior spinal nerves in Myxine are

described. Peripheral cell bodies in rr. ventrales and rr. dorsales of the most anterior spinal nerves in Myxine are described. Whether these cell bodies belong to the autonomic system seems uncertain.

12. The musculature of the piston mechanism in Myxine is homologized to that of Petromyzon. Certain similarities between the facialis musculature in Myxine and Petromyzon are pointed out. M. cornealis in Petromyzon is composed of a part innervated by spinal nerves and a part innervated from one of the cranial nerves.

13. Judging from the literature on the central nervous system and the sensory end organs in the Cyclostomes, and judging from the new data concerning the peripheral course of the cranial nerves set forth in the present paper, it seems unlikely that any end buds exist in the skin of the Cyclostomes.

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14. Some earlier writers have questioned the accuracy of a subdivision of the V_2-complex in Cyclostomes into a r. maxillaris and a r. mandibularis. According to STENSIÖ, the Cyclostomes are primary agnathous. The position of the nerve branches in relation to the buccal cavity may, however, justify a subdivision and, moreover, HOLMGREN has found a palatoquadrate in Myxine and compared the tooth plate cartilage in Myxine to the mandibular complex in certain fishes. In the present paper an attempt is made to subdivide the V_2-complex into maxillaris and mandibularis branches, but this subdivision could not be carried out completely. Thus it is possible that in the anatomy of the Cyclostomes we can trace the first vestiges of a subdivision into maxillaris and mandibularis branches, a subdivision which only becomes fully established in the Gnathostomes.

The primary subdivision of the V_2-complex in the Cyclostomes should be into nerves destined for the muscles, on the one hand, and those destined for the skin and the mucous membranes on the other. It seems doubtful whether a border-line ought to be drawn between branches destined for the skin and those destined for the mucous membranes, as a displacement of branches between these groups is easily envisaged during the course of the phylogenesis.

The subdivision suggested implies that little significance ought to be attached to the main direction of the trigeminal trunks. This, in its turn, implies that the piston mechanism in Myxine can be homologized to that in Petromyzon and that the embryonic muscle groups in embryonic Myxine can be compared to those in Petromyzon embryos.

Finally, certain special nerve branches in the V_2-complex of Myxine are compared to nerve branches in Petromyzon.

15. The relation between the trigeminus and the blood vessels and between the trigeminus and the skeleton in the Cyclostomes is discussed on the basis of the new interpretation of the trigeminus.

16. The branchial region lies much further rostral in the Cephalaspids than

in the Cyclostomes and the mandibular segment of the Cephalaspids is of about the same size as the other branchial segments. Starting from this, the author has advanced a new interpretation of the cranial nerves and some blood vessels in the Cephalaspids.

17. The differences between Myxine and Petromyzon in the innervation of the skin and the mucous membrane caudal to the trigeminal region and the differences between the anterior spinal nerves in the two Cyclostome groups may be attributed to the backwards migration of the gills in the Myxinids, described by DEAN and STOCKARD.

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XIX. ABBREVIATIONS.

a.con. anterior connection between the trabecle and the dorsal longitudinal bar.
a.l.p. anterior lateral plate.
a.m. arteria mandibularis.
a.pal. arteria palatina.
aud.c. auditory capsule.
br. brain.
buc.r. root of the buccalis.
card.h. cardinal heart.
ch. notochord.
com. bundle from the hyomandibularis, running to ramus cutaneus descendens.
corn.c. cornual cartilage.
d.l.b. dorsal longitudinal bar.
ex.hy. extra-hyal.
ex.mand. extra-mandibular.
f.b.pl. frontal basal plates.
f.f. fine calibre fibres.
g.buc. ganglion of the buccalis.
gill.p.I. most anterior gill pocket.
g.sac. saccular ganglion.
g.utr. utricular ganglion.
g.V trigeminal ganglion.
g.Vpal. part of the trigeminal ganglion, issuing r. palatinus.
g.VII facial ganglion. (In Petromyzon ganglion hypoticum.)
g.VIId. distal facial ganglion.
g.VIIp. proximal facial ganglion.
g.VIII acoustic ganglion.
hyp.c. hypophysial cartilage.
L lateral side.
l.a. lingual artery.
lab.c. labial cartilage.
lig.1,lig.2 etc. ligament 1, ligament 2 etc.
M medial side.
m.bas. musculus basilaris.
m.b.pl. medium paired basal plates.
m.b.t.l. musculus basali-tentaculo-labialis.
m.c. buccal cavity.

m.c.o. musculus copuloglossus obliquus.
m.constr.br. musculus constrictor branchialis externus.
m.cor. musculus coronarius.
m.corn.Ic. central fibre in the spinal-innervated part of musculus cornealis.
m.corn.Ip. parietal fibres in the spinal-innervated part of musculus cornealis.
m.corn.II part of m. cornealis, innervated by cranial nerves.
m.c.o.tend. tendon of m. copuloglossus obliquus.
m.cr.b. musculus cranio-basalis.
m.c.v. musculus craniovelaris.
met.r. roots of the metotic cranial nerves.
m.f.t. musculus flexor trabeculae.
m.i.v.p. musculus *infravélaire postérieur*.
m.l.c.b. musculus levator cartilaginis basalis.
m.nas. musculus nasalis.
mot. motor branch.
m.p.br. musculus praebranchialis.
m.p.c.b.a.,p. musculus protractor cartilaginis basalis anterior and posterior.
m.p.d.p.,s. musculus protractor dentium profundus and superficialis.
m.r.m.o. musculus retractor mucosae oris.
m.s.c. musculus spinosocopularis.
m.s.n.b. musculus subnasali-basalis.
m.s.n.n. musculus subnasali-nasalis.
m.s.n.t. musculus subnasali-tentacularis.
m.sp.v. musculus spinovelaris.
m.sup.oc. musculus supraocularis.
m.t.l. musculus tectolateralis.
m.t.o.com. ventral commissure of musculus transversus oris.
m.t.o.s.s. musculus transversus oris sensu stricto.
m.t.p. musculus tentacularis posterior.
m.tr.c. musculus trabeculo-coronarius.
m.tr.s.n.p. musculus trabeculo-subnasalis profundus.
m.tr.s.n.s. musculus trabeculo-subnasalis superficialis.
m.t.s.a. musculus tectospinosus anterior.
m.t.s.p. musculus tectospinosus posterior.
m.v.c. medial ventral cartilage (plate).
n.buc. nervus buccalis.
n.c. nasal capsule.
n.d. nasal duct.
n.h.d. naso-hypophysial duct.
n.l.p. nervus lateralis posterior.
n.oph. nervus ophthalmicus.
n.oph.I, II, III and *IIIa* branches of nervus ophthalmicus.
p. pocket (fold) in the digestive tract, lateral to the velum.
par.m. spinal muscle.
p.b. "palatine bar".
p.b.a. parabranchial artery.
per.c.b. peripheral cell bodies.
ph. pharynx.
pist.c. piston cartilage.
r.ap. ramus apicalis.
r.ap.I and *II* branches of r. apicalis.
r.bas. ramus basilaris.
r.bas.l. lateral branch of ramus basilaris.
r.bas.m. medial branch of ramus basilaris.
r.buc. ramus buccalis.
r.cut.d. ramus cutaneus descendens.
r.dent. ramus dentalis.
r.dent.I branch of ramus dentalis.
r.d.m. motor ramus dorsalis (rami dorsales).
r.d.s. sensory ramus dorsalis (rami dorsales).
r.etm. ramus etmoidalis.
r.ext. ramus externus.
r.ext.I branch of ramus externus.
r.hy. ramus hyomandibularis.
r.hy.br.d. dorsal branchial nerve bundle of ramus hyomandibularis.
r.hy.br.v. ventral branchial nerve bundle of ramus hyomandibularis.
r.hy.c. cutaneous branches of ramus hyomandibularis, running mainly rostrad.
r.m.a. ramus muscularis anterior.
r.m.a.I, II and *III* branches of ramus muscularis anterior.
r.mand. ramus mandibularis.
r.m.bas. ramus musculus basilaris.
r.m.b.t.l. ramus musculus basali-tentaculolabialis.
r.m.c.h. ramus musculus cranio-hyoideus.
r.m.c.o. ramus musculus copuloglossus obliquus.
r.m.cor. ramus musculus coronarius.
r.m.c.r.,a.g. ramus musculus copuloglossus rectus and musculus anuloglossus.
r.m.cr.b. ramus musculus cranio-basalis.
r.m.c.v. ramus musculus craniovelaris.
r.m.i.v.a. ramus musculus *vélaire ascendant*.
r.m.i.v.i.,v.b. ramus musculus *infravélaire inférieur* and musculus *vélaribranchial*.

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r.m.i.v.p.,c.a. ramus musculus *infravélaire postérieur* and musculus cardio-apicalis.
r.m.l.c.b. ramus musculus levator cartilaginis basalis.
r.m.nas. ramus musculus nasalis.
r.m.p. ramus muscularis posterior.
r.m.p.c.b.a. ramus musculus protractor cartilaginis basalis anterior.
r.m.p.c.b.p. ramus musculus protractor cartilaginis basalis posterior.
r.m.p.d.p.,s. ramus musculus protractor dentium profundus and superficialis.
r.m.ph. ramus musculus pharyngeus.
r.m.p.p. ramus musculus pharyngeus posterior and musculus *vélaire descendant.*
r.m.p.,t.l. ramus musculus pharyngeus and musculus tectolateralis.
r.m.r.l.p.,r.p. branch to *le releveur de la lèvre postérieure* and *le rétracteur des papilles.*
r.m.r.m.o. ramus musculus retractor mucosae oris.
r.m.s.c. ramus musculus spinosocopularis.
r.m.s.n.b. ramus musculus subnasali-basalis.
r.m.s.n.t. ramus musculus subnasali-tentacularis.
r.m.sp.v. ramus musculus spinovelaris.
r.m.t.,c.,p. ramus musculus tubulatus, musculus clavatus and musculus perpendicularis.
r.m.t.o.,s.n.n. ramus musculus transversus oris and musculus subnasali-nasalis.
r.m.t.p. ramus musculus tentacularis posterior.
r.m.tr.c. ramus musculus trabeculo-coronarius.
r.m.tr.s.n.p. ramus musculus trabeculo-subnasalis profundus.
r.m.tr.s.n.s. ramus musculus trabeculo-subnasalis superficialis.
r.m.t.s.a. ramus musculus tectospinosus anterior.
*r.m.t.s.p.*ramus musculus tectospinosus posterior.
r.m.t.v. ramus musculus *tectovélaire.*
r.m.v.a. ramus musculus *vélari-apical.*
r.m.v.c. ramus musculus velocranialis.
r.m.v.g.,b.g. ramus musculus *vélariglosse* and musculus basilariglossus.
r.pal. ramus palatinus.
r.pal.I, II, IIa, III, IIIa trunks (branches) of r. palatinus.
r.pal.I,oph? dorsal trunk of r. palatinus, probably carrying in addition some ophthalmic fibres.
r.per. ramus perforans.
r.p.h. ramus posthyoideus.
r.p.o. ramus postorbitalis IX.
r.rec.ap. (*r.rec.*) ramus recurrens rami apicalis.
r.rec.VII ramus recurrens facialis.
rr.m.vel. rami musculares velares.
rr.v.b. rami velobuccales.
rr.v.b.I, II, III, IV and *V* branches of rami velobuccales.
r.sub.oc. ramus subocularis.
r.sub.p. ramus subpharyngeus.
r.su.op. ramus subopticus.
r.su.op.m. motor part of ramus subopticus.
r.su.op.s. sensory part of ramus subopticus.
r.su.or. ramus suborbitalis.
r.sup.oc. ramus supraocularis.
r.sup.p. ramus suprapharyngeus.
r.sy.br. ramus sympathico-branchialis.
r.tend. branch to a tendon.
r.tent.I, II, III and *IV* ramus tentaculi I etc.
r.v. ramus ventralis (rami ventrales).
r.v.I most anterior ramus ventralis.
r.vel. ramus velaris.
s.b.d. branch, lost on the inner side of the gutter-shaped, caudal basal plate.
s.b.v. branch, lost ventral to the medium paired basal plates.
sens. sensory branch.
sens.VII sensory fibres in nervus facialis.
s.n.b. subnasal cartilage.
s.oc.f. subocular fenestra.
sp.comp. most anterior spinal nerve complex.
sty.c. stylet cartilage.
symp. autonomic or visceral afferent spinal nerve branch.
tent.c.I, II and *III* tentacular cartilage I etc.
tr. trabecle.
v.ao. ventral aorta.
ves. vesicular supporting tissue.
II optic nerve.
III oculomotor nerve.
IV trochlear nerve.

Vm.r. motor trigeminal root.
Vm.r.1 and *2* parts of the motor trigeminal root.
Vs.r. sensory trigeminal root.
V—VII commissure from the facial to the trigeminal ganglia.
V—VIIcut skin branches from the facial-trigeminal commissure.
VI (*VI=3*) abducens nerve.
VIr. root of the abducens nerve.
VII facial nerve
VIIr. facial root.
IX glossopharyngeus.
IXv.r. ventral skin branch from glossopharyngeus.
X vagus.

CONTRIBUTIONS TO THE QUESTION OF THE ORIGIN OF TETRAPODS

BY

NILS HOLMGREN

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In my paper "On the origin of the tetrapod limb" (1933) I came to the conclusion that "Stegocephalians, anurans, reptiles, birds and mammals belong to a tetrapod group which has originated from fish ancestors, probably crossopterygians, with dichotomically branched pectoral fin skeleton, whereas the urodeles must be considered to have originated from fish ancestors, (crossopterygian or dipnoan), with a short biserially arranged archipterygium".

"The construction and development of the limbs give strong support to the opinion, that the amphibians do not form a homogenous systematic unit, but have arisen at least diphyletically. The *Urodela* must be cut off from the other amphibians as a tetrapod class of its own . . ."

The idea of a relationship between dipnoans and amphibians was not a new one. HAECKEL, M. FÜRBRINGER, KERR, BRIDGE, SEMON, K. FÜRBRINGER, SEWERTZOFF, GOODRICH and others have pointed out the great agreement between dipnoans and amphibians, an agreement they find so striking, that a real and near relationship must exist between these two groups.

A number of investigations led WINTREBERT (1910, 1922) to the conclusion

that the amphibians are developed polyphyletically: "Les faits recueillis dans l'ontogénie des Salamandridae, rapprochés de ceux qui montrent dans le crâne des Urodèles adultes une architecture tout à fait spéciale, inclinent à penser que l'origine des Amphibiens est polyphylétique, en ce sens que les Urodèles et les Stégocéphales proviennent de souches différentes." (1922, p. 419).

The idea of the independence of the *Urodela* from the other amphibians and relationship with the Dipnoi was accepted by SÄVE-SÖDERBERG (1935), who classified the Urodela together with the Dipnoi. It was also accepted by JARVIK (1948), with the difference, however, that he derived the urodeles from porolepiform and the stegocephalians and anurans from osteolepiform crossopterygians. KINDAHL (1937) by investigating the development of the kidneys, came to the conclusion that there was no obstacle in the way for assuming a near relationship between the Dipnoi and the Urodela, especially the *Necturus*. WICKBOM (1944, 1948), studying the chromosome-conditions, found a greater concordance between Dipnoi and the Urodela than between the latter and the anurans. In his investigation on the brain of dipnoans and amphibians RUDEBECK (1945) says (p. 142): "The morphology and ontogenetic development of telencephalon in lungfishes and Amphibians have so many things in common that there is reason to believe that the amphibian forebrain has originated from a braintype which may have been closely related to that existing in primitive Dipnoans. This is especially the case in the Urodela." PEHRSON (1949) and HOLMGREN and PEHRSON (1949) found in the sensory line system of the head a great agreement between the recent *Dipnoi* and the *Urodela*, a minor between the former and the *Anura*.

There thus seems to be a distinct increase of the arguments in favour of my interpretation of the Urodela as nearly related to the dipnoans.

In the present paper I intend to demonstrate that there are also in the skeleton of the head certain traits which decidedly connect the two classes with each other.

A. SOME STATEMENTS CONCERNING THE SKULL IN *PROTOPTERUS* AND *NEOCERATODUS*.

Before entering upon a comparison between the dipnoan and the urodelian skull, it is necessary to try an embryological analysis of the former.

THE CHONDROCRANIUM.

In the chondrocranium of the early embryo (for instance in a 17.5 mm embryo of *Protopterus*) we may state the following facts (fig. 1):

1) The broad parachordal plate and the very big auditory capsules.

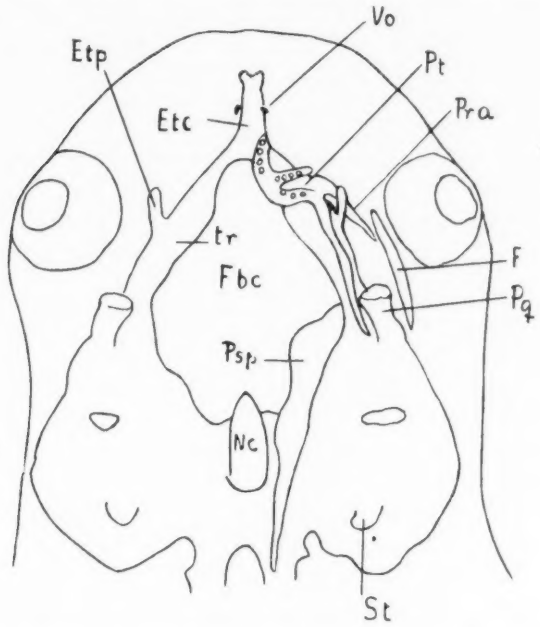

Fig. 1. Skull of embryo of *Protopterus annectens* 17.5 mm; ventral view; graphical reconstruction.

2) The very broad basicranial fenestra.

3) The rather long trabecles which converge strongly frontad and join to form an unpaired, rostrumlike ethmoidal commissure ending with a paired blastematic part frontally (cornua trabecularia). In a 60 mm larva the rostrum-like ethmoidal plate is paired apically. At the frontal border of the "pterygoid" tooth-plate the perichondrium of the ethmoid rod (plate) sends down a strong lamella between the two foremost tooth-ridges. More caudally, between the ridges this lamella has lost its connection with the ethmoid rod but continues as a vertical chondroid lamella (a kind of intertrabecle) between the tooth-ridges, forming a mesial attachement to them.

4) The presence at about the middle of the trabecle of a "lamina orbitonasalis" or "antorbital" or "ethmoidal" process (figs. 1, 2, *Etp*). This process is situated just in front of the point where the rudimentary palatine process of the palatoquadrate joins the trabecle.

5) The nasal capsules are not covered by any dermal bone (figs. 3, 4). They consist of a lattice-work of cartilage.

6) The autostylic quadrate cartilage (fig. 2), with otic, basal and ascending processes. The palatine process is represented by a ligamentous band in *Neoceratodus*.

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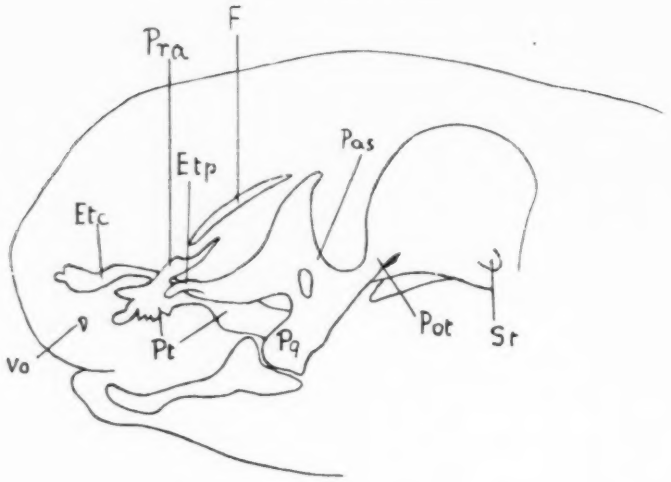

Fig. 2. The same skull; side view.

7) The high spheno-lateral plates (fig. 2) (alisphenoid plates, "pila antotica"), which later join the auditory capsules.

8) The auditory fenestra, lying rather far caudally on the lower surface of the auditory capsule, is quite open in early stages. In the 17.5 mm stage of *Protopterus* it is closed from the front by a tongue of cartilage (figs. 1, 2, *St*), apparently growing out from its anterior margin. In the adult the place of the former fenestra is well discernible as a rounded space where the cartilage seems to have another consistency than its surroundings.

9) That space of the cranial wall where a petrosal, if present, ought to be developed, is quite cartilaginous.

10) The space of an orbitosphenoid is also cartilaginous.

11) In *Protopterus* there are 2 spino-occipital nerves, in *Neoceratodus* 4.

THE DERMAL SKULL.

The skull roof.

The dermal skull roof is in some characteristics so different in *Neoceratodus* and *Protopterus*, that it must be considered separately in these genera. In HOLMGREN and STENSIÖ (1936) we have described the cranial roof of *Neoceratodus* (fig. 4) as consisting of three longitudinal lines of bone plates, viz. an unpaired medial, consisting of a postrostral plate frontally and a medial fronto-parietal caudally, a paired lateral fronto-parietal and a supratemporo-intertemporal. In addition a dermosphenotic and occasionally some extra-

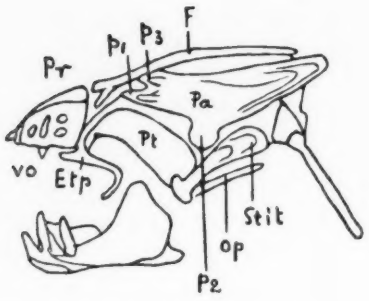

Fig. 3. Skull of adult *Lepidosiren paradoxa*; side view.

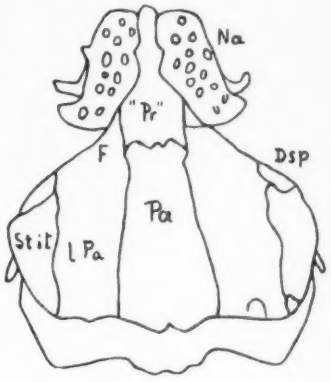

Fig. 4. Skull of *Neoceratodus Forsteri*; dorsal view.

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scapular plates are present. The terminology of these plates rests upon the conditions in palaeozoic Dipnoans (HOLMGREN and STENSIÖ).

In *Protopterus* and *Lepidosiren* the dermal roof (fig. 3) was described as consisting of the postrostral, the so called supraorbital and the supratemporo-intertemporal bones. The fronto-parietal was considered as being of endocranial origin.

The supraorbital was compared with the lateral frontoparietal of *Neoceratodus* and the medial fronto-parietal was represented by the tough connective tissue membrane between the two "supraorbitals".

The embryological analysis of the dermal skull roof leads in *Protopterus* to the following results:

1. The postrostral arises from two paired centers viz. a *rostral* or prenasal rod, ossifying along its lateral borders and a pair of somewhat protruding postrostral plates (called nasals in fossils), ossifying from in front and laterally. These plates cover the two big bulbi olfactorii of the brain.

2. Behind the two postrostrals in the young fish (50—60 mm) lie two somewhat protruding plates (fig. 5). These ossify from separate centres. They cover the telencephalon.

3. On the outside of these plates lies the narrowed frontal part of a big plate which widens considerably caudad and ends by narrowing on a level with the posterior border of the endocranium (fig. 5). At the border between this lateral plate and the medial plate just mentioned, a strong, flat process is sent down to cover the outside of the ascending process of the "pterygoid". The medial plate, the process and the lateral plate form together the "supraorbital" bone.

4. Behind the medial plate of the "supraorbital" bone in the young larva lies an oblong unpaired plate covering the space between the two lateral plates

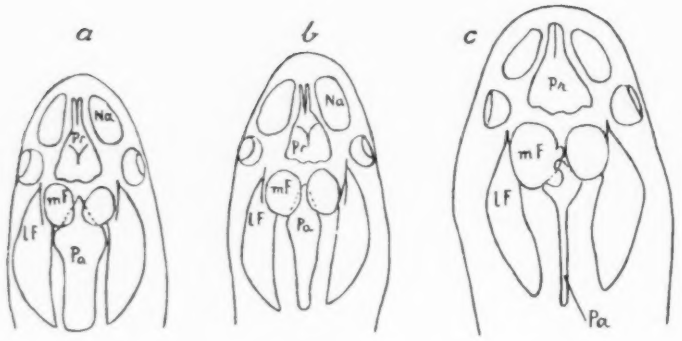

Fig. 5 a, b, c. Larval dermal skulls of three somewhat different stages of *Protopterus annectens*; dorsal view.

(fig. 5 a). It lies level with these plates and in the same strong connective tissue membrane as they. This plate, in older larvae (fig. 5 b and c), sinks down below this membrane and connects with the neural skull, there forming the unpaired socalled frontoparietal bone, which thus is of dermal origin. In *Lepidosiren* (40 mm stage) this bone is distinctly paired. A process developed on the lateral margin of the anterior portion of the "supraorbital" bone in adult fishes may represent the dermosphenotic.

In adult specimens the "fronto-parietal" (fig. 3, *Pa*) bone is intimately connected with the endocranium. It has three processes (p_1, p_2, p_3), two of which are directed frontad (p_1, p_3). They are situated below the "supraorbital" bone and are covered by its basal part. The third (p_2), which is very distinct in *Lepidosiren*, is only represented in the adult *Protopterus* by a broad protuberance at the lateral border of the "frontoparietal" bone. In *Lepidosiren* this process lies upon the surface of the ascending process of the palatoquadrate (fig. 3). It was interpreted as the alisphenoid pedicle in HOLMGREN and STENSIÖ (1936) as it has the same relations to nerves and blood-vessels as a true alisphenoid pedicle. (At that time I believed that the "fronto-parietal" bone was of endocranial origin.)

From about the basis of this process a broad lamella of the "fronto-parietal" bone runs down on the inside of the cartilaginous parts of the skull to meet the ascending lamella of the parasphenoid bone, forming together with this lamella the lateral wall of the cranial cavity in that region of the skull.

5. A bone lamella covering the outside of the otic process of the palatoquadrate cartilage (probably) represents the supratemporo-intertemporal bone (fig. 3).

6. Lacking in the skull roof are: premaxillary, maxillary, nasal and prefrontal bones.

The dermal skull roof of the adult *Neoceratodus* differs considerably from

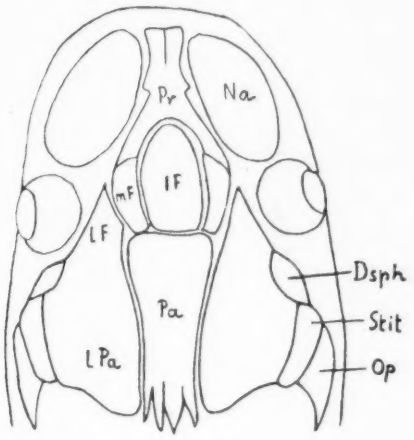

Fig. 6. Skull of larval, 8 months old, *Neoceratodus*; dorsal view.

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that in *Protopterus*, but an investigation on a young fish of 10—12 months of age (fig. 6) shows that it is built up according to the same pattern as in the larva of *Protopterus*. In the adult *Neoceratodus* there are two unpaired bones in the midline, viz. the "postrostral" and the "medial fronto-parietal" bone.

An embryological analysis of the "postrostral" gives the following surprising result. It consists of four different components (fig. 6). 1) The rostral rod, in a 10 months old larva is distinctly differentiated from the postrostral plate. 2) The triangular, apparently paired postrostral plate ("nasals") from the postero-lateral corners of which issues on each side a posterior ribbon, which fronto-laterally embraces a big medial plate (fig. 6, *IF*), developed dorsally to the forebrain. At the basis of this ribbon the postrostral plate has an angular process (present also in the adult). 3) A big unpaired medial plate (fig. 6, *IF*). 4) On each side of about the two posterior thirds of the medial plate lies an oblong plate (*mF*) following the curve of the lateral border of the medial plate to its posterior end, where it abuts against the frontal corners of the "medial fronto parietal" bone (*Pa*). Frontally the bone extends to the posterior end of the posterior ribbons of the postrostral plate.

Compared with *Protopterus* it is obvious that the rostral rod and the postrostral plate are corresponding structures. But the two other structures of the complex, its lateral and medial caudal plates, are not immediately recognised. The lateral of these borders (caudo)laterally on the frontal end of the "lateral fronto-parietal" and at this point the processus ascendens of the pterygoid reaches the cranial roof and a lamella from the latter extends down outside this process. This point answers to the limit between the paired medial frontal and the lateral frontal in *Protopterus*. From this fact it may be concluded that the structures meeting at this point are homologous. Then remains the big

medial plate. This plate has no homologue in *Protopterus*,[1] but in fossil Dipnoi, such as *Dipterus* and *Ctenodus*, corresponding plates may be present, named "central frontals" or "interfrontals".

The big posterior medial plate (*Pa*) — called medial fronto-parietal — in *Neoceratodus* answers perfectly to the parietal (fronto-parietal) in *Protopterus*. The difference is, however, that whereas it sinks down to the endocranium in *Protopterus*, it retains its superficial position in *Neoceratodus*.

The "lateral fronto-parietal" in *Neoceratodus* well corresponds, at least frontally, to the big lateral plate in the *Protopterus*-larva. In *Neoceratodus*, where a sensory line canal is present, the lateral frontoparietal chiefly consists frontally of the medial lamella of sensory line bones belonging to the supraorbital line and caudally of the medial lamella of the supratemporo-intertemporal (answering to the "parietal" of *Polypterus*). The dermo-sphenotic of *Neoceratodus* seems to be represented by a process of the "supraorbital" in *Protopterus*. The homologies are summarized in the table on next page.

Dermal bones of the mouth cavity.

The dermal bones of the mouth cavity are in *Neoceratodus* as well as in *Protopterus:* the vomeral tooth and bone, the pterygoid and the parasphenoid bones.

1. On each side of the rostrumlike ethmoidal plate and widely separated from it lies a tooth rudiment in a 17.5 mm embryo of *Protopterus* (figs. 1, 2, *Vo*). This is the primordium of the vomeral tooth. In *Neoceratodus* a bone plate, vomer, develops at a corresponding place and to this plate a transversal series of teeth is attached. In *Protopterus* only one tooth develops on each side and is found near the medial line in the adult, a short distance behind the nostrils.

2. The pterygoid of the adult *Protopterus* carries the great pterygoid tooth-plate frontally. As a support to this plate a very strong ascending process is developed (figs. 1, 2, *Pra*), which extends dorsally along the lower surface of the "supraorbital" bone of the skull roof. From the processus ascendens and the tooth-plate, the pterygoid (*Pt*) continues caudad and broadens to a strong plate inside the palato-quadrate. In the embryo the tooth-plate develops simultaneously with the ascending process. At that time (14.2 mm embryo) the body of the pterygoid is very insignificant, extending from below the tooth caudad to a point immediately *in front of* the "antorbital" process (*Etp*). The tooth-plate is thus situated ontogenetically in front of this process. In a 14.3 mm embryo the pterygoid has developed further caudad, and in a 15 mm embryo it has arrived at the inside of the palato-quadrate. That part of the pterygoid

[1] In a specimen of *Protopterus* two small bone elements (fig. 5 c) were separating from one of the medial frontals in the space between them. Such elements may indicate the possibility of interfrontals or "anamestic" bones in *Protopterus* as well.

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	Neoceratodus	Protopterus		*Some fossil Dipnoi* (Watson & Gill)	*Urodeles* (*Necturus*)
Post-rostrale	*rostral rod*	*rostral rod*	Postrostral	*internasal* (*Ctenodus*)	*rostral rods* in *Siren*
	postrostrals	*postrostrals*		*nasals* (*Ctenodus, Sagenodus* and others)	—
	interfrontal	—		*interfrontal* (*Ctenodus*)	—
	medial frontals	*medial frontals*		*frontals* (*Ctenodus*) *interfrontal* (*Sagenodus, Conchopoma*)	*medial frontal* absent or fused with lateral frontals
Fronto-parietale laterale	*lateral frontals*: prefrontal portion	*lateral frontals*	Supraorbital	*prefrontals*	*lateral frontals*
	frontal portion	—		*intertemporals*	
	lateral parietals (supratemporo-intertemporal medial lamella; *Polypterus*-parietal)	*?lateral parietals* (posterior portion of lateral frontals)		?	—
Fronto-parietale mediale	*medial parietal* (*Amia*-parietal) superficial	*medial parietal* (joined with endocranium) paired in *Lepidosiren*		*parietal*	*parietals* (paired)
	supratemporo-intertemporal (lateral lamella)	*supratemporo-intertemporal*		supratemporo-intertemporals or intertemporals (Holmgren & Stensiö) (not named by Watson & Gill)	"*quadratojugal*"
	opercular	*opercular*		*opercular*	"*squamosal*"
	dermosphenotic	dermosphenotic process of lateral frontals		*squamosal*	—
	extrascapular	—		*tabular*	—
	—	—		premaxillary in *Dipterus, Phaneropleuron, Uronemus?*	*premaxillary*
	—	—		maxillary in *Dipterus, Phaneropleuron, Uronemus?*	*maxillary* (absent in perennibranchiates)
	—	—		—	*petrosum*
	—	—		?	*nasals, prefrontals* (absent in perennibranchiates)
	pterygo-palatine	pterygo-palatine		pterygo-palatine	pterygoid + palatine
	vomer	vomer (reduced)		vomer	vomer
	parasphenoid	parasphenoid		parasphenoid	parasphenoid
	dental	dental		preangulo-angular	dental
	scale on lip cartilage	—		"dentary" (in *Dipterus*)	—
	prearticular	prearticular		prearticular	prearticular (gonial)
	splenials	splenial (articulo-splenial)		splenials	articulo-angular
	coronoids (dental plate)	coronoid (dental plate)		dental plate	coronoid

which develops behind the "antorbital" process follows in *Neoceratodus* the rudimentary (mesenchymatic) palatine process of the palato-quadrate.

3. The parasphenoid of the adult *Protopterus* is a frontally broad triangular plate caudally narrowing and extending below the occipital region of the skull. Frontally it ends abruptly at a fair distance behind the tooth-plate. The anterior part of the basicranial fenestra is thus not covered by the parasphenoid. In an embryo of 17.5 mm body length it is clearly seen that the parasphenoid is originally paired, developing from behind frontad (fig. 1). The parasphenoid develops in *Protopterus* an ascending vertical process or lamella *which takes part* in the formation of the wall of the brain cavity in the orbito-temporal region. Outside this lamella the parasphenoid continues with a broad horizontal shelf underlying the orbito-temporal region and the anterior part of the auditory capsule. In *Neoceratodus* the parasphenoid covers the entire palatine surface, and has no ascending lamella.

The mandible.

The ossified parts of the mandible are well known. But besides these there are cartilaginous parts which seem to be rather little known. These parts belong to the Meckelian cartilage. As there are important differences between the mandibles of *Neoceratodus* and *Protopterus*, they will be dealt with separately.

Neoceratodus.

On the mandible the following membrane bones have been recorded:

1. The "preangulo-angular" (fig. 7, *Dent*), covering the entire lateral surface of the Meckelian cartilage, 2. the prearticular part on the inside of the mandible, forming the osseous part of the symphysis dorsally to the 3. splenial-postsplenial (*Sppsp*), which thus covers the symphysis ventrally. 4. The splenialia, consisting of 4—5 very small sensory line bones, of which the foremost is joined with the spleniale-postspleniale. To these wellknown bones may be added: 5. the coronoid, a thick dental plate carrying the big teeth. It must be considered as a separate bone, as the corresponding plate in *Protopterus*-larvae has a certain independence at least caudally. The coronoid is joined to the prearticular with the dorsal edge of which the dental plate is fused. 6. Laterally on the dorsal side of the expanded lateral part of the Meckelian cartilage (symphysial plate) lies in 8—10 months old embryos a short rodlike bone, carrying two very small teeth. This bone probably belongs more to the skin of the lower lip than to the mandibular skeleton and seems to agree more with a placoid scale than with a skeletal membrane bone.

The Meckelian cartilage is not ossified in any part. Caudally it begins with its strong articular portion. Then follows its strong rodlike middle portion. This part is seen between the preangulo-angular (*Dent*) and prearticular bones,

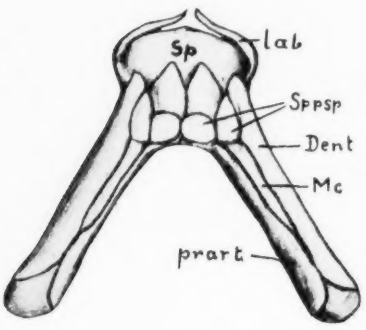

Fig. 7. Lower jaw of *Neoceratodus;* ventral view.

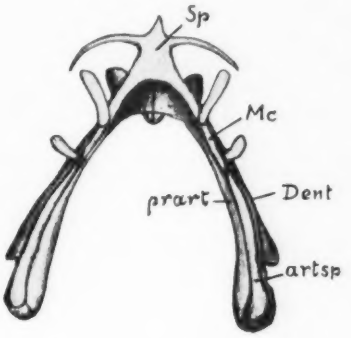

Fig. 8. Lower jaw of *Protopterus annectens*; ventral view.

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which meet only for a short extent caudally. In the region of the big dental plate the cartilage is seen from the dorsal side outside the plate. In front of this point the two Meckelian cartilages meet with a broad and rather long symphysial plate (*Sp*). This plate lies just in front of the symphysis of the prearticular bones about in front of the anterior border of the splenial-postsplenial. The preangulo-angular (*Dent*) ends laterally on the ventral surface of the cartilaginous symphysial plate.

The lateral part of the symphysial plate is very interesting as it has a cylindrical border. This swollen border frontally merges into a kind of tentacle (labial cartilage) (*lab*) which runs fronto-mediad close to the frontal edge of the symphysial plate, the tips of the contra-lateral tentacles reaching the midline, where they bend off frontad. Dorsal to the swollen part of the lateral border lies close to the lip-epithelium the small scale-like bone with its 2 teeth mentioned above. In young fishes, where the lip-cartilage has not yet developed, the proximal part of the symphysial cartilage shows a border thickening. At this thickening and along the edge extends frontad a mesenchymatous string, which may be the primordium of the swollen part of the border and the free part of the lip-cartilage. Inside this string the cartilage is seen to proliferate in some places. The probable significance of these structures will be mentioned below.

Protopterus.

In *Protopterus* corresponding bony elements are present (fig. 8), with the exception, however, of the lip-scale. The splenial series here consists of a long splint-like bone situated on the ventrolateral side along the Meckelian cartilage (fig. 8, *artsp*). This bone does not reach the mandibular symphysis frontally. The mandibular sensory line runs along the surface of this bone and I therefore believe that it is the membranous component of a reduced

series of sensory line bones (as those in *Neoceratodus*). Caudally this bone runs out on the ventrolateral surface of the articular process of the Meckelian cartilage and there comes in very close contact with the cartilage. In a 60 mm embryo there is only a very thin perichondrium between the bone and the cartilage. This bone may thus be considered to be an articulare-spleniale.

In *Protopterus* there is a medial ventral paired bone foreshadowing a spleniale-postspleniale, but it is possible that it is not a separate bone as it develops in continuity of the prearticular bone. The osseous symphysis is formed by the "preangulo-angular" (*Dent*) and the prearticular, which both meet with their vis à vis. The articular part of the Meckelian cartilage is very strong, ossified only in connection with the articulare-spleniale. The medium part of the cartilage (*Mc*) is a rather narrow rod, only seen in the frontal half of the jaw between the "preangulo-angular" and the splenial. Level with the second big tooth of the tooth-plate the Meckelian cartilage issues from its bony surroundings and becomes a free cartilage. It then proceeds frontad as a cartilage band to join its partner of the other side, forming a strong triangular symphysial plate (*Sp*), quite free from the osseous symphysis. The anterior corner of this plate forms a strong rostral process on each side of which the plate extends a long process following the outline of the lower lip. At the point, where the frontal end of the trabecle issues from its bony surroundings, another rodlike process is sent out to meet the first-named process. A third similar but shorter cartilage is connected with the Meckelian cartilage at the point where it becomes invisible caudally. These three cartilages are labial cartilages developed in connection with the jaw-cartilage (cf. AGAR 1906). Compared with *Neoceratodus* it is obvious that the median rostral rod of *Protopterus* answers to a short and broad process in *Neoceratodus*, weakly developed in young fishes. The first lip-cartilage in *Protopterus* probably corresponds with the lip cartilage of *Neoceratodus*, described above. The second and third lip cartilages in *Protopterus* have no counterpart in *Neoceratodus*.

When compared with some fossils of dipnoans (for instance *Sagenodus* and *Ctenodus*), it is obvious that the anterior part of the lower jaw there must have contained a cartilaginous symphysial plate in front of the foremost membrane bones. In *Dipterus* (fig. 9) this cartilage was ossified and carried the so called dentary. "The dentaries are small elements forming a rim to the anterior end of the mandible; the two bones are indistinguishably fused. In section their outer surface forms nearly three quadrants of a circle passing smoothly from the lower upward into the oral surface; this surface is covered with the shiny punctate surface now recognized as characteristic of a cosmoid bone. This region projects forward and is sharply marked off from the rest of the lower jaw by depressions on the nearly vertical lateral surfaces." (WATSON and GILL 1922, p. 207—208.) This description of the "dentary" makes it very probable that it is no true dentary, as it is covered with a cosmoid

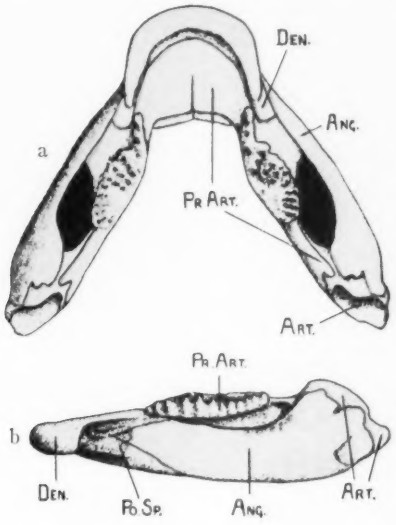

Fig. 9. Lower jaw of *Dipterus*; a: dorsal view; b: side view (From WATSON and GILL 1923).

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layer, which must belong to an integumental structure, viz. a layer, of fused scales, developed upon the lower lip more or less in an analogous manner as the horny rim on the edge of the lower lip in *Siren*. If this conclusion is correct, the little integumentary scale described in a somewhat corresponding position in *Neoceratodus* would be a remnant of the scales of the cosmoid layer in *Dipterus*.

An explanation of the *Dipterus* conditions may be possible from the conditions in *Neoceratodus*, described in preceding lines. In *Dipterus* the symphysial plate of the Meckelian cartilages was undoubtedly ossified. It had a cylindrical rim around its lateral and frontal borders. In *Neoceratodus* such a rim is present on the lateral margin of the symphysial plate and it bears teeth (probably quite integumental). The difference is then that the rim of *Neoceratodus* extends frontally into a labial cartilage, which, however, follows the plate closely. Imagine that this labial cartilage was fused on to the symphysial plate and ossified together with it, and the *Dipterus*-conditions would be realized.

According to this theory the "dentary" is no dentary and we must accordingly search for a real dentary in another jawbone. On the outside of the jaw lies the "preangulo-angular". As this bone is pierced in *Sagenodus* and *Ctenodus* and also in *Dipterus* by foramina for sensory canal tubes belonging to the mandibular canal, it is obvious that this bone must contain a splenial bone in its ventral part. Comparing with the Crossopterygians, where this series of bones is well-known, lying ventrally to the dental (dentary), we are compelled to assume that the "preangulo-angular" also contains a dental. Thus I

come to the conclusion that the outside of the Meckelian cartilage is covered by a composed bone: spleniale-dentale-(angulare). As, however, the dentale and angulare are never separate in the recent lungfish and do not develop from separate primordia in the embryos, I am obliged to believe that there is no angular present at all, but that the dentale-spleniale extends along the whole Meckelian cartilage of *Dipterus* and the other fossils mentioned above. In *Neoceratodus* the "preangulo-angular" has no splenial portion, either in the adult or in any embryonic stage. Therefore this bone must be a dental. The mandibular sensory canal runs outside this dental and not in it as in the fossils. In *Protopterus*, where articulare-spleniale is an independent bone, the "preangulo-angular" is a dental, as in many fishes and in amphibians.

Thus the principal bones of the lower jaw of the recent dipnoans are: in *Neoceratodus* the dental and the prearticular and in *Protopterus* the dental, the prearticular and the articulare-spleniale. The prearticular of *Protopterus* is pierced posteriorly by a foramen, located as is the foramen for the chorda tympani (mandibularis internus) in amphibians, but I could not find any nerve in it.

Additional notes on the supratemporo-intertemporal and on the opercular apparatus.

In *Neoceratodus* the supratemporo-intertemporal ("Squamosum") consists of two parts: a larger superficial triangular plate (fig. 4, *Stit*) from the lower anterior corner of which issues a long process covering the outside of the palatoquadrate (otic process). The otic and glossopharyngeal part of the sensory line of the head runs along the upper (medial) border of the superficial plate.

In *Protopterus* and *Lepidosiren* (fig. 3) the supratemporo-intertemporal chiefly consists of that portion which lies upon the palatoquadrate. The lower portion of it is broadened to a big rounded plate, which becomes intimately connected with the cartilage of the palatoquadrate at the lateral border of its articular head. Its upper end is also broadened where it covers a part of the outside of the otical region of the skull.

The large operculum of *Neoceratodus* is connected with the caudo-lateral border of the supratemporo-intertemporal (fig. 6). Its anterior end does not reach the lower end of the quadrate.

In *Protopterus* and *Lepidosiren* the operculum is rodlike (fig. 3). Frontally it reaches the palatoquadrate behind and somewhat below and outside of the broad frontal portion of the supratemporo-intertemporal. From this point the opercular rod runs caudad diverging from the supratemporo-intertemporal.

The subopercular in *Neoceratodus* as well as in *Protopterus* is more or less rodlike and has no close connection with the palatoquadrate, but is strongly connected with the keratohyal.

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B. SOME STATEMENTS CONCERNING THE SKULL IN URODELES, ESPECIALLY IN *NECTURUS* AND COMPARISON WITH THE DIPNOANS.

For comparison with the lungfishes I have especially used *Necturus* and the other perennibranchiate urodeles. In selecting these urodeles I have disregarded the hypothesis of these urodeles as being throughout neotenic types, an hypothesis which I regard as not being sufficiently supported by anatomical facts. The neoteny hypothesis seems to be based chiefly on the presence of a certain metamorphosis in the urodeles, a metamorphosis which is very much belated in the axolotl, (where a real neoteny occurs) and occasionally, for instance, in *Triturus*. Considering the skull, the metamorphosis consists chiefly of the transformation of the position of the vomeral and pterygio-palatine teeth. In the unmetamorphosed (larval) specimens these teeth form a longitudinal row parallel to the premaxillary and maxillary series of teeth (WIEDERSHEIM 1877). In the metamorphosed specimen the vomero-palatine teeth lie transversally or longitudinally caudad. This position is correlated to the platelike development of the frontolateral portion of the vomer, which has caused the altered direction of the tooth series (cf. WINTREBERT 1922). In the perennibranchiates the vomer and palatine teeth are arranged as in the larval axolotl. This condition could be given as a reason for considering the perennibranchiates as neotenic types, which have lost their metamorphosis. But the fact that in such old-fashioned genera as *Amphiuma, Megalobatrachus* and *Cryptobranchus,* which are decidedly not neotenic, the vomeral conditions are chiefly the same as in the larval axolotl and in the perennibranchiates, speaks against the neoteny hypothesis and in favour of primitive conditions in the latter.

THE CHONDROCRANIUM OF THE LARVAL *NECTURUS* AND OTHER URODELES.

1. The parachordal plate (fig. 10) is broad as in the Dipnoi.
2. The basicranial fenestra is broad, but not as broad as in the living Dipnoi, where the skull is relatively much shorter than in *Necturus*.
3. The trabecles are very long, generally, but slightly converging frontad.[1] In this condition *Necturus* differs from the Dipnoi, but here the shortness of the latter's skull may also play some part. The trabecles are joined somewhat behind their tips by means of a short ethmoidal plate (*Etc*). Also in the Dipnoi the tips of the trabeculare are free, forming trabecular

[1] In *Amphiuma* the trabecles converge strongly and the fenestra basicranialis is unusually broad. The same is the case for instance in a very young (7.5 mm) axolotl (STÖHR).

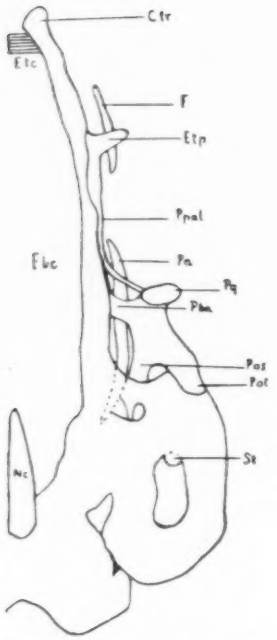

Fig. 10. Skull of embryonic *Necturus maculatus* (20 mm); ventral view.

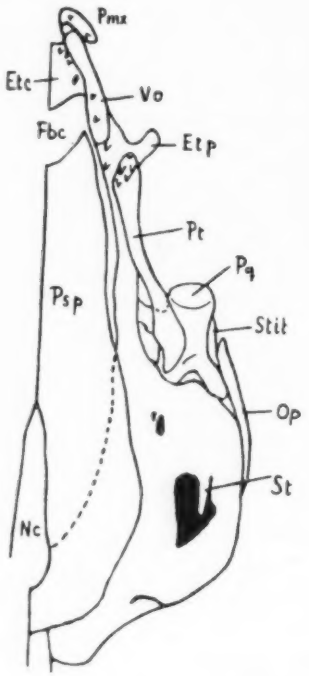

Fig. 11. Skull of embryonic *Necturus* (24 mm); ventral view.

cornua. In *Siren* a short medial rostral rod is present (young specimens and adults). In *Necturus* (27 mm larva) (fig. 11) the ethmoid plate is connected with a somewhat chondroid tissue extending caudad below it between the foremost vomeral teeth. In *Amphiuma* this tissue chondrifies. This tissue may be compared with the chondroid lamella in *Protopterus*, mentioned in preceding pages.

4. The presence of an "antorbital" or ethmoid process ("lamina orbitonasalis") is common to all urodeles (and anurans) (figs. 10, 11, *Etp*) and the Dipnoi, but it is not recorded in any other fish group. This process belongs to the palatine process (pterygoid process) of the palatoquadrate (fig. 10, *Ppal*). It may be compared with the morphologically anterior labial cartilage in sharks, which is also related to the palatine process of the palatoquadrate.[1]
5. The nasal capsules are uncovered (fig. 12 b) and consist of a latticework of cartilage rods in the perennibranchiates as well as in the recent Dipnoi.

[1] The labial cartilage of *Polypterus* may, however, belong to the palatine process of the palatoquadrate, but has become widely separated from it.

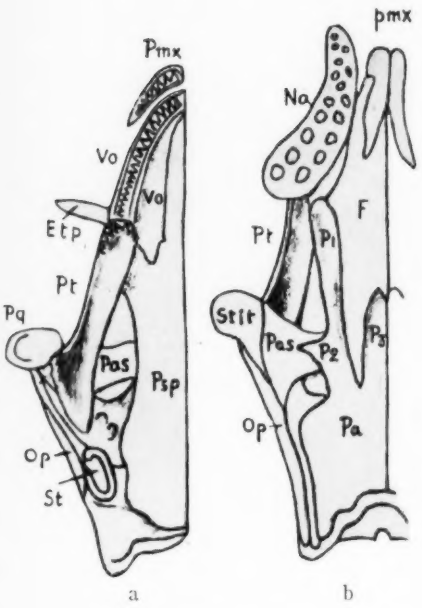

Fig. 12. Skull of adult *Necturus*; a: ventral; b: dorsal view. (From WIEDERSHEIM.)

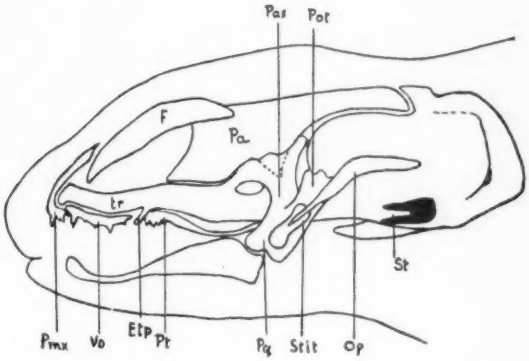

Fig. 13. Embryonic skull of *Necturus* (24 mm); side view.

6. The autostylic quadrate (fig. 13) cartilage is common to *Necturus* (and the other urodeles) and the Dipnoi, but not in the same sense in any other group of fishes.
7. Characteristic for *Necturus* (and other urodeles) is the rather high sphenolateral region of the embryo (fig. 13), which connects with the auditory capsule by means of a posterior tænia marginalis. Later it joins with the capsule altogether. In *Protopterus* the corresponding portion is comparatively higher. A tenia marginalis also develops here, but the complete junction of the sphenolateral plate with the auditory capsule occurs earlier here than in *Necturus*.
8. In the auditory fenestra a stapes develops in the urodeles; it is in the 24 mm embryo frontally continuous with the cartilage of the auditory capsule (figs. 10, 11, 13). In *Protopterus* the fenestra closes from in front by means of a cartilaginous tongue (fig. 1). The place of the former auditory fenestra, however, is always discernible in *Protopterus* (and *Neoceratodus*) through the transparency of the closing cartilage. Its position fully corresponds with that in the urodeles.
9. In the urodeles a portion of the auditory capsule ossifies as a "petrosal". Such an ossification is not present in the Dipnoi.

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10. In most urodeles an "orbitosphenoid" is present. This bone, however, is absent in *Necturus*. In the Dipnoi the space of the orbitosphenoid is occupied by cartilage only.
11. The urodeles have two spinoccipital nerves. The same is the case in *Protopterus*, but not in *Neoceratodus*, where four are present.

THE DERMAL SKULL.

The skull roof.

In the perennibranchiates the skull roof consists of three paired bones. They are the dorsal portion of the premaxillary, the frontal and the parietal bones. The "squamosal" may also be reckoned as belonging to the roof, but that bone will be considered later together with the opercular complex. In the other urodeles the nasal, prefrontal and the maxillary bones are added.

1. There is no "postrostral" present in the urodeles with the exception of *Siren*, where the two so-called accessory premaxillaries are very suggestive of the paired anterior rostral rods of the "postrostral" in *Protopterus*. As in *Protopterus* they lie dorso-laterally on the anterior end of the ethmoid plate. The posterior expanded part of the postrostral of *Protopterus* does not seem to be represented in the urodeles or to be included in the anterior end of the frontal.[1]

2. The frontal bone is very long in *Necturus*, extending caudally over the anterior half of the parietal in the adult (fig. 12 b). In the embryos it is much shorter (fig. 13, *F*). Frontally it lies below the dorsal lamella of the premaxillary. The frontal of the adult urodeles is a simple bone lamella throughout its entire length. Dorso-frontally the two frontals meet in the midline, where they are connected with each other by a strong tendinous tissue. In an embryo of 24 mm body length, however, the two ossifying frontals are widely separated frontally, but connected, however, by means of a connective tissue membrane covering the forebrain dorsally. This membrane later (27 mm stage) ossifies in continuity with the frontals and forms the medial part of them. Thus it is possible to interpret the frontal of *Necturus* as a structure composed of a lateral and a medial portion. The lateral part of this compound frontal narrows considerably and bends down frontally to meet (in the 27 mm stage) the *vomer* near its frontal end. The development and relations of the frontal in *Necturus* (and probably in other urodeles) may be interpreted as the "supraorbital" in *Protopterus*. The part of the frontal appearing first in *Necturus* corresponds to the lateral plate of the "supraorbital" in *Protopterus*. This part in both genera comes in contact with the tooth-bearing part of the palatine-pterygoid bar (see

[1] According to HERTWIG the frontal process of the premaxillary develops from a separate primordium, which later fuses with the toothbearing part of the premaxillary.

below). The medial part of the "supraorbital" in *Protopterus* may be compared with the medio-frontal portion of the frontal in *Necturus*.

3. The parietal bone of *Necturus* originally forms in the same connective tissue layer as the frontal, but later sinks down to a lower level and successively grows out frontally below the frontal (fig. 12 b). This mode of development is the same as in *Protopterus*. In both cases the parietal thus forms a roof over the cranial cavity. In *Necturus* the parietal develops three well defined processes, two frontal (p_1, p_3) and one lateral (p_2). The processes are: 1. a medial frontal (p_3) lying close to the medial line. It affords a certain support to the frontal. 2. A longer lateral (p_1), which in the adult extends to the nasal region It reaches laterally to the trabecles (in the embryo) and the taenia marginalis (fig. 13), inside of which a ridge will ultimately form the lateral wall of the cranial cavity. 3. The lateral process (fig. 12 b, p_2) of the parietal forms a triangular covering upon the upper half of the ascending process of the palatoquadrate. Comparing with *Protopterus* and *Lepidosiren* we find most striking agreements. The three processes (fig. 3) are present — as stated above. The medial frontal process (p_3) forms a support to the frontal part of the "supraorbital" (frontal). In addition it meets the socalled processus ascendens of the "pterygoid" bone. The lateral frontal process (p_1), which is shorter than the dorsal, reaches the trabecula. The lateral process is not well-developed in *Protopterus*, but in *Lepidosiren* it is a big flat process (p_2) covering the processus ascendens as in *Necturus*.

Thus the parietal is principally the same in *Protopterus* and *Necturus* (and other urodeles also). There is, however, the difference that it is unpaired in *Protopterus*, whereas it is paired in *Necturus*. This difference, however, is bridged over in *Lepidosiren*, where the parietal is distinctly paired in a 40 mm specimen.

4. The outside of the otic process and part of the "petrosum" of *Necturus* are covered by the "squamosal" and the "quadrato-jugal" bones. These bones will be considered later together with the opercular complex.

5. In the perennibranchiates maxillary, nasal and prefrontal bones are lacking in the skull roof. In *Protopterus* and *Neoceratodus* the same are missing and in addition the premaxillary. A maxillary and a premaxillary may be present in some palaeozoic dipnoans (see p. 20).

The dermal bones of the mouth cavity in *Necturus* (and other urodeles), compared with those in *Dipnoi*.

The following bones are present in the roof of the mouth cavity in *Necturus:* the premaxillary, the vomer, the pterygoid and the parasphenoid. Maxillary (and separate palatine) bones are absent.

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1. The toothbearing part of the premaxillary originates in a mesenchymatic tissue mass with tooth-bases situated in front of and somewhat below the anterior end of the cornua trabecularia (anterior tips of the trabeculae in front of the trabecular commissure). In a 24 mm stage the palatine as well as the frontal part are present (fig. 11). In *Protopterus*, where cornua trabecularia are present as well, there is no such bone present at any stage of development. As, however, premaxillary bones have been found in some fossil dipnoans (*Dipterus, Phaneropleuron, Uronemus?*), *Protopterus* as well as *Neoceratodus* may have reduced their premaxillary bones. The loss of the maxillary bone in *Protopterus* and in the perennibranchiates may perhaps be due to convergency.

2. The vomer and the pterygoid may conveniently be dealt with together. The vomer of *Necturus* develops from a mesenchymatic string ventrally to the trabecle *in front of* the ethmoidal process. Its anterior portion lies level with the trabecular commissure (24 mm embryo, fig. 11). The pterygoid on the other hand develops along the palatine process of the palatoquadrate, *behind* the antorbital process. In younger stages of development (20—22 mm embryos) it was stated that the development of the vomer begins from in front and has reached the antorbital process before the beginning of the development of the pterygoid, which subsequently grows backward to the inside of the palatoquadrate. As already stated the "vomer" of the recent lungfishes develops on the lower side of the frontally fused trabeculae (ethmoid commissure) and therefore ought to correspond with the vomer in *Necturus*. But it was also stated that the big pterygoid tooth develops in front of the antorbital process and thus cannot be a pterygoid tooth, which ought to develop on that part of the pterygoid bone which originates on the palatine process of the palatoquadrate. Now the question arises: what is the "pterygoid" tooth-plate. Ontogenetically it develops in front of the antorbital process and therefore should not be a pterygoid tooth-plate. Its origin would proclaim it to be a vomer, but a vomer is already present in front as "vomer". Then there only remains the possibility that it is a palatine tooth-plate, comparable with the "palatine tooth-plate" in *Siren* (fig. 14, *pal*). The dermopalatine in fishes develops upon the frontal end of the palatine process (where many times an autopalatine is present). In fishes this dermopalatine very often grows out to cover parts which lie outside its place of origin. So may have been the case in *Siren*, where the anterior part of the palatine extends frontad beyond the antorbital process, and so may perhaps have been the case in the Dipnoans. In *Fleurantia*, GRAHAM-SMITH and WESTOLL (1937) have found a rather long narrow bone provided with granular teeth. They name it provisionally "dermopalatine". Tooth-bearing bones of somewhat similar appearance have been found in *Phaneropleuron* and *Uronemus* and have there been called "maxillae" or "premaxillae".

Thus lacking the possibility of making a *detailed* comparison between the

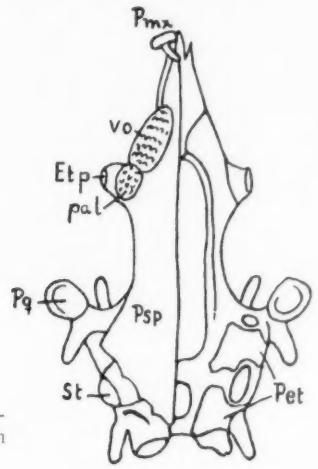

Fig. 14. Skull of adult *Siren lacertina*; ventral view. (From WIEDERSHEIM 1877.)

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vomero-palatine-pterygoid complex in urodeles and dipnoans, I must content myself with the statement that this complex *as a whole* is built up according to the same pattern in these two animal groups, and that the pterygoid tooth-plate in dipnoans is rather a palatine than a pterygoid tooth-plate.

3. The parasphenoid of a 24 mm *Necturus* is a broad flat plate covering the basicranial fenestra, excepting its foremost part (fig. 11). Later it will cover the whole fenestra. In the orbito-temporal region it has an ascending lamella on the inside of the cartilage of this part. The parasphenoid originates from paired primordia. In all these characters it behaves as the parasphenoid in the dipnoans. A difference, however, is its considerable backward extension below the anterior part of the spinal chord in dipnoans. Thus the parasphenoid is strongly pointed posteriorly in the lungfishes, but generally more rounded in the urodeles. (In *Siren* it ends with a rather sharp angle, fig. 14).

The "squamosal" and the "quadrato-jugal" in urodeles and dipnoans.

The corpus of the palatoquadrate of *Necturus* is covered on its lateral (dorsal) side by a nearly circular bone plate from which a process is extended for a short distance along the otic process. This bone has been called the quadrato-jugal ("quadrato-maxillary") bone. Outside this bone and covering it from near its frontal end lies a second bone, the "squamosal" or "tympanicum" or "paraquadratum" of the authors. This bone is a long flattened narrow bone, which continues caudad upon the dorsolateral surface of the skull to its extreme caudal end.

The "quadratojugal" bone is so closely connected with the quadrate cartilage frontally, that there is no perichondrium between the cartilage and the bone. Its process, however, behaves as a normal membrane bone.

Studying the embryonic development of these bones we find the first primordium of the "quadrato-jugal" closely adhering frontally to the quadrate cartilage, whereas the "squamosal" is fairly distant from it, lying laterally (in a 24 mm stage) or ventrolaterally (in 23 mm stage) to it.

Comparing with *Protopterus* and *Lepidosiren* (fig. 3) the explanation of these bones cannot be any other than the following:

1. The "quadrato-jugal" is the intertemporo-supratemporal of the Dipnoi, especially of *Protopterus* and *Lepidosiren*. Its relations to the quadrate cartilage makes this statement manifest.

2. The "squamosal" is no squamosal, as a real squamosal ought to be developed in relation to the jugal sensory line. The "squamosal" of the urodeles cannot be any other bone than the opercular bone.

If we look at the embryonic development of the opercular in *Protopterus* we shall find the anterior end of its primordium ventrolateral to the primordium of the "quadrato-jugal" about as in *Necturus*, but from this foremost point the rudiment extends caudad in *Protopterus*, dorso-caudad in *Necturus*. The difference depends upon the dorsal part of the constrictor hyoidei muscle, which expands between the two bones in *Protopterus* and is lacking in *Necturus*. As the dorsal part of the muscle disappeared the two bones were drawn together. In *Siren*, where the "quadrato-jugal" is said to be missing (STADTMÜLLER 1936) its proximal part is present but joined to the "squamosal".

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The lower jaw.

In *Necturus* and most other urodeles the membrane bones of the jaw are the dentale, the prearticulare and the two toothbearing coronoids. The dentale covers the outside, the prearticulare (goniale) the inside and the tooth-bearing coronoids the upper surface. This is also the arrangement in *Protopterus* with the difference, however, that there is also the articulare-spleniale. But a bone answering perfectly to the latter is present in *Megalobatrachus, Cryptobranchus, Onychodactylus* (fig. 15), *Ranodon* and *Hynobius*, thus in primitive urodelians. In the amphibians the bone is generally named articulo-angulare.

The Meckelian cartilage of *Necturus* forms the strong articular head caudally while frontally it forms a short but broad symphysial plate, which is provided with a medial process frontally around which the foremost part of the dentale is developed, here connecting the cartilage immediately.

In *Siren*, where the lower lip is provided with a very strong horny ridge, the dentale extends a dorso-lateral lamella, which follows the ridge on its inside, affording it strong support. This lamella is somewhat fenestrated.

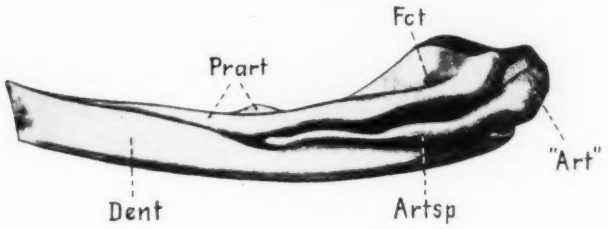

Fig. 15. Lower jaw of *Onychodactylus japonicus*; ventral view. (From STADTMÜLLER 1936.)

The preceding comparison between the recent lungfishes and urodeles seems to make it very probable (if not certain) that there is a rather close relationship between the Dipnoi and the urodeles. The agreement of most cranial structures is so striking that any other explanation must be rejected. There is, however, a considerable difference, as the big crushing palatine teeth in Dipnoi are substituted in the urodeles by small, conical teeth placed together on the palatine or on the frontal end of the pterygoid bone. In *Siren* the palatine teeth form more or less transversal series on the entire surface of the palatine, forming a palatine tooth-plate.[1] With the presence of the big palatine tooth in the Dipnoi is correlated the strong development of the pterygoid and the big ascending process of its palatine part. This difference between the recent Dipnoi and the urodeles is to a certain degree bridged over by the conditions in *Conchopoma* (Upper Carboniferous), *Uronemus* (Lower Carboniferous) and *Fleurantia* (Upper Devonian), where the palatine teeth were not developed as such crushing teeth as in most other Dipnoi. In *Conchopoma* the "pterygoid" was narrow frontally and had small teeth irregularly arranged. In *Uronemus* there was a marginal series of large, compressed, conical teeth and a very large number of small, almost hemispherical denticles covering a narrow area within the margin (WATSON and GILL 1922) and in *Fleurantia* there are a few rows of bigger teeth together with numerous small denticles. WATSON and GILL are inclined to explain the teeth conditions in *Conchopoma* and *Uronemus* by assuming that their originally strong tooth-plates broke up into smaller units. "*Semon* showed that in development the dentition of *Ceratodus* begins as a series of isolated denticles supported by a network of bony spicules, and that the tooth-plates of the adult are built up by the confluence of such denticles." "This mode of development is consistent with the view that *Uronemus* may have arisen from a form with tooth-plates, because its isolated denticles may merely result from the carrying on to adult life of a structure which occured in larval stages. It is possible that a stage with distinct unfused denticles formed a larger part of the life-history in early Dipnoi than it does

[1] The *tooth-plates* of the Dipnoi as well as those of the urodeles are partly built up of tooth-bases.

in *Ceratodus*." (WATSON and GILL, p. 214). I think that this explanation is quite correct and probably the only one. The *Uronemus* and *Conchopoma* are with regard to the teeth "neotenic" lungfishes in the same sense as the perennibranchiates are "neotenic" and according to my opinion the perennibranchiates (and other urodeles) have developed from such "neotenic" Dipnoi. It is not excluded that these "neotenic" genera formed a line of descent parallel with the *Protopterus*-line, with practically corresponding reduction for instance of the dermal roof of the skull. This "neotenic" line must not have been very long, because it must have issued from a stem where the sensory line bones were already reduced or reducing. Such fossil dipnoans, however, are not known. Therefore we must rely upon those facts which it may be possible to gather from *Conchopoma* and *Uronemus*. Both these genera have a number of sensory line bones. Imagining these bones reduced, there will remain the following bones in the skull roof of *Conchopoma:* 1. two large (sometimes fused) "nasals" (terminology of WATSON and GILL). These "nasals" correspond to the postrostrals in *Protopterus*. As the postrostrals develop in a protecting position to the bulbi olfactorii, the nasals, when present, to the nasal sacs, the dipnoan "nasals" may not be true nasals. 2. one large unpaired "interfrontal". This interfrontal is probably of paired origin. 3. paired "frontals" + "intertemporals", sometimes fused in *Scaumenacia*, lying lateral to the medial frontal ("interfrontal") and extending past the "interfrontal" frontally as well as caudally, and 4. a medial parietal, reaching the caudal border of the skull roof. This set of bone plates corresponds perfectly with the bone plates, which compose the skull roof in the larva of *Protopterus*.

As to the "interfrontal" it is rather probable that there are two different bones, which have got this name. The large "interfrontal" of *Conchopoma* and *Sagenodus*, which meets the "parietal" caudally must be different from the small "interfrontal" in *Ctenodus* and *Uronemus*, which meets the medial frontals caudally. The "interfrontal" of the former is probably the fused medial frontals of the latter, as in some specimens of *Scaumenacia*. Then the small interfrontal in *Uronemus* must be an anterior socalled central frontal (STENSIÖ, anamestic bone WESTOLL), of which the older dipnoans had a rich supply (*Dipterus*). Symmetrically-arranged protuberances at the posterior margin of the postrostral in *Protopterus* may perhaps contain elements corresponding with the transversal row behind the postrostrals in some *Dipterus* specimens (HOLMGREN and STENSIÖ, p. 366, fig. 280 A).

In addition there seems in *Conchopoma* to be a certain reduction of the sensory line bones, as far as could be stated from WATSON and GILL's picture and description. The "squamosal" (dermosphenotic), however, was large, but a bone in front of it, called "prefrontal", was small and there were no traces of circumorbital bones and premaxilla (but a paired "dentary" was present). A supratempero-intertemporal seems to have been present, with which the

operculum articulated. The bone called tabular may perhaps represent a part of the medial lamella of the supratemporo-intertemporal. These conditions are very suggestive of those in *Neoceratodus* and *Protopterus*. Also the broad, shovel-shaped, flat parasphenoid reminds one of the conditions in *Protopterus*.

I imagine that the perennibranchiate urodeles may have arisen from dipnoans, which have belonged more or less to the *Conchopoma*-type, but with more reduced sensory line bones and with solitary conical teeth scattered upon the anterior part of the "pterygoid". This type may have had a broad parasphenoid devoid of teeth and probably a premaxillary as well and perhaps also a maxillary, as in *Phaneropleuron* and *Uronemus*. In most other cranial features the ancestors of the perennibranchiates must have been built principally as *Protopterus*.[1]

The agreements between the recent dipnoans (*Protopterus, Neoceratodus*) and the urodeles (especially perennibranchiates) are too great to be explained through convergency.

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[1] Concerning the phylogenetic position of *Protopterus* the following statements regarding the tooth-plates may be of some interest. In *Protopterus* the tooth-plates in the upper as well as in the lower jaw consist of three tooth-ridges on each side, viz. a frontal, a lateral and a caudo-laterally directed ridge. This pattern is already developed in young embryos and does not change during their whole life. In *Neoceratodus* the tooth-plates in both jaws of the young larvae have the same three ridges as those of *Protopterus*. But in old specimens there are six ridges present, new ridges being added at the posterior end of the larval tooth-plates. As all extinct dipnoans with tooth-plates have a considerable number of ridges on their tooth-plates, we must assume that *Protopterus* has retained the embryonic state of the tooth-plates, thus being "neotenic" in that respect.

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ABBREVIATIONS.

Ang dentale (angulare)
"Art" articulare in Amphibians
art sp articulo-spleniale
Art sp articulo-angulare in Amphibians
Ctr cornu trabeculare
Den "dentary"
Dent dentale
Dsp dermosphenotic
Etc ethmoid commissure
Etp ethmoid process
F frontale
Fbc fenestra basicranialia
IF interfrontale
Lab labial cartilage
lF lateral frontal
lPa lateral parietal
Mc Meckel's cartilage
mF medial frontal
Na Nasal capsule
Nc Notochord
op operculum
p_1, p_2, p_3 processes of the parietal
Pa parietal
pal palatinum
Pas proc. ascendens of palatoquadrate
Pba processus basalis of palatoquadrate
Pet petrosum
Pmx premaxillare
Po sp postspleniale
Pot processus oticus of palatoquadrate
Ppal processus palatinus
Pq palatoquadrate
Pr postrostrale
Pra processus ascendens of pterygoid
prart prearticulare
Prart prearticulare (goniale)
Psp parasphenoid
Pt pterygoid
Sp symphysial plate
Sppsp spleniale-postspleniale
St stapes
Stit supratemporo-intertemporale
tr trabecula
Vo vomer

ON THE TETRAPOD LIMB PROBLEM—AGAIN

BY

NILS HOLMGREN

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In a preceding paper (1949) I have compared the cranial structures and their development in Dipnoi and Urodela in order to find out if such a comparison could lend support to my theory regarding the double origin of the amphibians viz. the derivation of the urodeles from dipnoans and the stegocephalians and all other tetrapods from crossopterygians.

In my papers on the tetrapod limb (1933, 1939) I have derived the evolution of the urodele limb from a dipnoan "archipterygium", that of the other tetrapods from a dichotomically-branched crossopterygian paddle. My theory has met with a certain amount of critic especially from GREGORY and RAVEN (1941) and WESTOLL (1943), who tried to explain the development of the limbs of all tetrapods from a crossopterygian paddle like that of *Eusthenopteron*.

When I (1933 and 1939) examined the question of the origin of the tetrapod limb I was impressed by GREGORY, MINER and NOBLE'S (1923) derivation of the tetrapod limb from the *Sauripterus* paddle. In this derivation the preaxial branch on the distal end of the second mesomere was considered to form the intermedium-centrale axis of the tetrapod limb. I was also impressed by the fact that the second joint in the *Neoceratodus* fin was composed of three portions which could answer to the radius, ulna and ulnare in tetra-

pods. In *Neoceratodus* the selachian meso-pterygium could be thought to have produced the long main axis (through "secondary polyisomerism"), whereas the metapterygial axis became strongly reduced. In *Neoceratodus* the intermedium-centrale axis is a linear line of skeletal elements as that in urodeles, in *Sauripterus* a dichotomiously branched tree as that in the other tetrapods. From this difference and many others I tried to deduce a double origin of the tetrapod limb.

GREGORY'S AND WESTOLL'S THEORIES.

Meanwhile GREGORY in a paper written together with RAVEN (1941)[1] altered his standpoint regarding the intermedium-centrale axis of the tetrapods, now considering this axis to form the postaxial border of the *Sauripterus* or *Eusthenopteron* paddle. The intermedium-centrale axis of his earlier papers was considered to have been lost. GREGORY and RAVEN based their derivation of the tetrapod limb upon the conditions in the *Eusthenopteron* paddle.

WESTOLL (1941) shared GREGORY'S and RAVEN'S opinion regarding the intermedium-centrale axis and his starting point was also the paddle of *Eusthenopteron*, partly because it was considered that the type ancestral to the tetrapod limb was not so expanded as the *Sauripterus* paddle, and because he considered it better adapted for a diagram suitable to all tetrapods.

When WESTOLL says that "the entire basis of HOLMGREN'S argument is removed by the recognition of the inturning of the mesomeral axis" viz. that the postaxial border axis of the paddle is the intermedium-centrale axis of the tetrapod limb, I cannot share this opinion as it is not sufficiently based on facts, but works with a lot of assumptions. Here I will only introductorily exemplify this with the following remarks. In the *Neoceratodus* paddle the second joint (the future ulna) carries preaxially the long main axis of the paddle and on the postaxial side a growing out portion (the future ulnare). In the crossopterygians the second mesomere (the future ulna) carries preaxially a rodlike "radial" (in *Eusthenopteron*) or the basal part of a (dichotomous) system of radials (in *Sauripterus*) and postaxially the two apical joints of the mesomeral axis (m_3 and m_4) with their end radial. On the postaxial side of the second mesomere, WESTOLL has added a process not present in any crossopterygian, which he declares to be the future ulnare. I have written this in order to exemplify that the basis of my earlier arguments is not entirely removed, as will also be shown in some detail further on. On the following pages I will take up the question with the same method as WESTOLL, and with *Eusthenopteron* (and *Sauripterus*) as a starting point, *strictly applying the theory to the ascertained facts* (and not the facts to the theory). Curiously

[1] GREGORY'S standpoint was another in his paper of 1935.

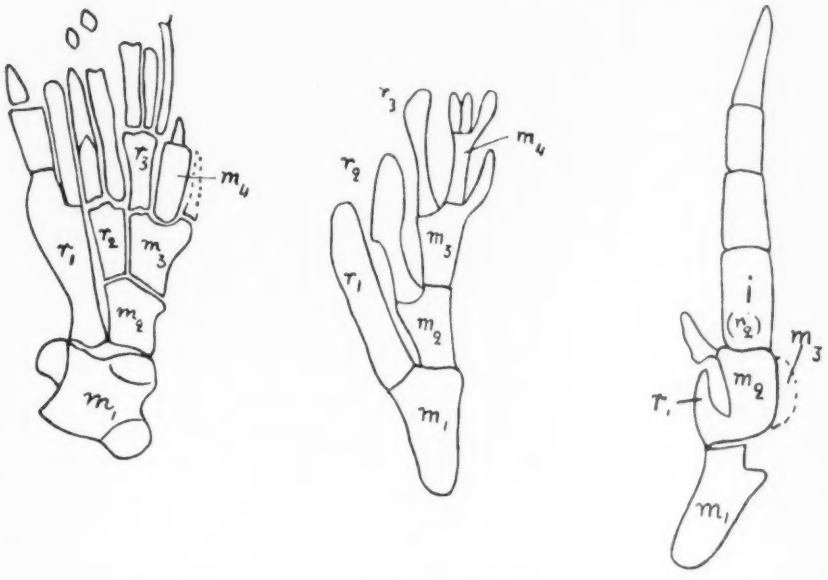

Fig. 1. Fig. 2. Fig. 3.

Figs. 1—3. Fig. 1. The *Sauripterus* paddle, diagram according to Gregory and Raven (1941). Fig. 2. The *Eusthenopteron* paddle (Holmgren, 1939). Fig. 3. Embryonic pectoral fin of *Neoceratodus*.

enough we shall see that from this standpoint we come to similar results, that I had arrived at fifteen years ago, viz. that there are two different types of tetrapod limbs, the one related to the dipnoan, the other to the crossopterygian paddle.

CRITICAL ANALYSIS OF WESTOLL'S THEORY.

It is obvious that a theory on the origin of the tetrapod limb must be based upon the features characteristical of *Sauripterus, Eusthenopteron* and *Neoceratodus* (*Epiceratodus*)[1] and on the ontogenetical development of the tetrapod limb. Of the mentioned three fish genera only *Neoceratodus* can give us an account of the embryological development of the fin skeleton. In the pictures figs. 1, 2 and 3 the *Sauripterus* (fig. 1) and *Eusthenopteron* (fig. 2) fin skeleton and the embryonic fin of *Neoceratodus* (fig. 3) are reproduced. The first-named fin skeleton is taken from the revised reconstruction of Gregory and Raven (1941) (fig. 4), the second from a photographical picture

[1] The simplified structure of the fins in *Protopterus* and *Lepidosiren* is not suitable for a basis of a theory on the tetrapod limb.

Fig. 4. The *Sauripterus* paddle. Gregory and Ravens reconstruction.

in my paper (1933) and the third also from the same paper. In the pictures I have used the lettering of WESTOLL (1943) as far as possible. I do not intend to give a full description of these pictures, only pointing out some points of interest. The dichotomy of the *Sauripterus* fin is almost complete. That of *Eusthenopteron* is also well pronounced but much less elaborate than that of the former and in *Neoceratodus* no dichotomy is seen at all. In the two crossopterygians four mesomeres are present.[1] The preaxial radials (r_2 and r_3) are simple in *Eusthenopteron* (fig. 2), each provided with two "rays" in *Sauripterus* (fig. 1). The mesomere 4 has in both crossopterygians two end rays each. In *Eusthenopteron* the mesomeres m_3 and m_4 have each a postaxial process, but m_2 has none. Such a process, but separated from m_3, is present in *Sauripterus*, but m_2 and m_4 have none. In the larval *Neoceratodus* less than three months old, the pectoral fin consists of a series of six elements. The second of these is deeply cleft from the apex to near the basis on the preaxial side owing to the basal fusion whith it of a primary preaxial piece. On the preaxial apical corner of the second joint of the stem a short ray is present.

[1] WESTOLL says *five* in *Eusthenopteron*, *four* (or *five*) in *Sauripterus*. He thus seems to have counted the two end radials as the fifth. In his diagrammatical pictures (fig. 1) of three stages possible in structural modification of the skeleton of the paddle six mesomeres are represented.

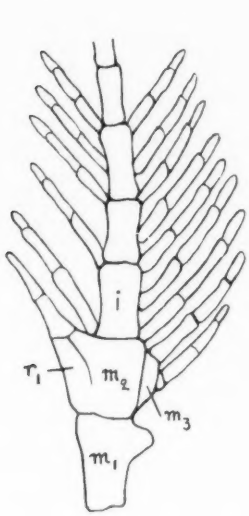

Fig. 5.

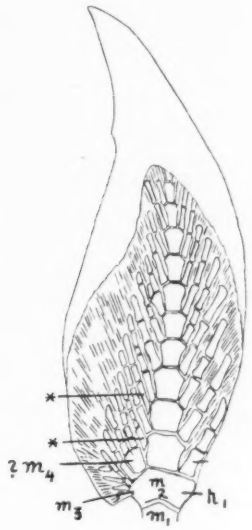

Fig. 6.

Figs. 5—6. Fig. 5. Pelvic fin of *Neoceratodus*. (Original.) Fig. 6. Pectoral fin of *Neoceratodus*. (Holmgren, 1933).

This ray in the actual stage of development is about to shift over to the apex of the original preaxial ray (r_1). In a pelvic fin of an adult *Neoceratodus* a perfectly similar disposition of a corresponding ray was met with (fig. 5). This ray may correspond to the ray r_2 in *Eusthenopteron* and to the dichotomus complex r_2 in *Sauripterus*[1]. This statement should imply a confirmation of WESTOLL's theory of the possible heterogenous nature of the preaxial ray in tetrapods, but WESTOLL's theory presumed that the ray r_2 had disappeared and that the ray r_3 had associated with the original preaxial ray (r_1). WESTOLL's presumption that also a r_4 may have entered the preaxial stem (fig. 7), cannot be sustained as there is no such ray in *Eusthenopteron*, the two end rays of the mesomeral stem in his pictures being used up to form his mesomere 5 (fig. 7). In WESTOLL's pictures of the possible relationship between the rhipidistian paddle and the tetrapod limb the m_3 and m_4 carry the proximal and distal postcentrals (p_3 and p_4) respectively. The m_3 should be the "intermedium" of the tetrapod limb. But in the tetrapod limb the intermedium *never* carries any postaxial appendix. If we consider the two accessory centrals of certain urodeles as representing such postcentrals, they ought to be p_4 and p_5 respectively (not p_3 and p_4). But p_5 is not present in the rhipidistian paddle.

[1] But it is also probable that the ray r_3 is an ordinary digit shifting over to the end of the preaxial radial, or which has—as an originally separate digit rudiment—chanced to form an articulation both with the m_2 and with the r_1.

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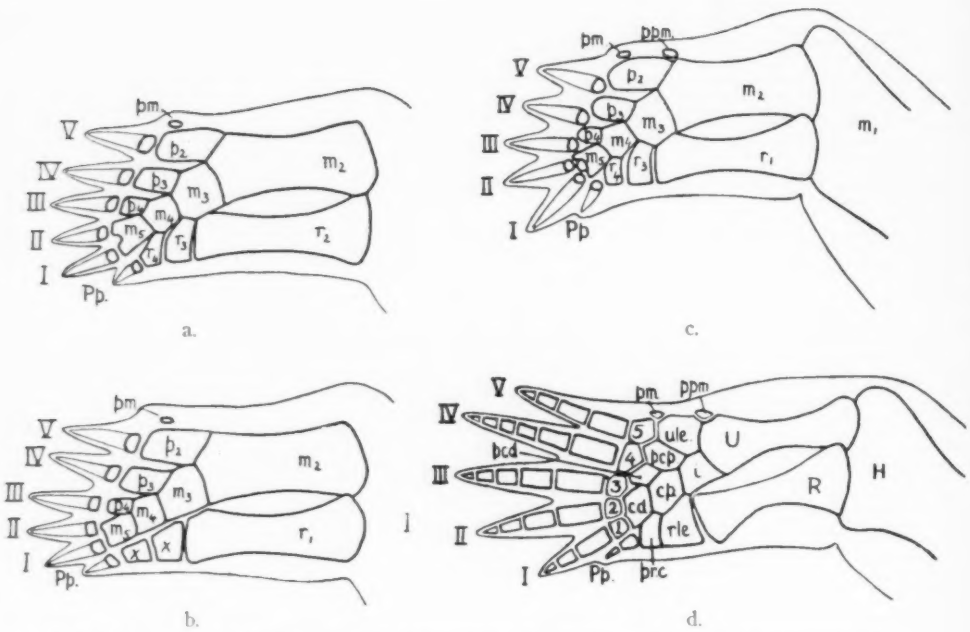

Fig. 7 a—d. Westoll's diagrammatical (alternative) representations of the development of the tetrapod limb, derived from the *Eusthenopteron* paddle.

Nor does this paddle contain a p_2, which is assumed to form the ulnare of the tetrapod limb, but as *Neoceratodus* has a postaxial outgrowth (m_3) on m_2, it is not excluded (from WESTOLL's standpoint) that it may also belong to the general rhipidistide pattern, but that is only an assumption. Thus, a tetrapod limb, constructed on the basis of the *Eusthenopteron* fin could not contain more than one postcentral, viz. the proximal (p_4) and the p_3 (belonging to the intermedium) must have been lost during the transformation period. It must be of some interest to point out that the third and the fourth joints of *Neoceratodus* each carry at their mid a small postaxial process as well in a 5 months old larva. In the adult this process forms the basis of the two mid rays always present (fig. 6, *) in pectoral fins on these joints. In an adult pelvic fin of *Neoceratodus* such midrays were present on the third, fourth and fifth joint (fig. 5) and in another also on the sixth. On the preaxial side the fifth had such a ray in the former fin and the fourth and sixth in the other. I assumed (1933) that the second joint of *Neoceratodus* was composed of two parts, the future ulna and intermedium, and then the next two represented two centrals each with its accessory central. This assumption was based on the conditions in urodeles. Now turning our attention to the end portion of the mesomeral axis of the crossopterygians, we find that the m_4 has a postaxial

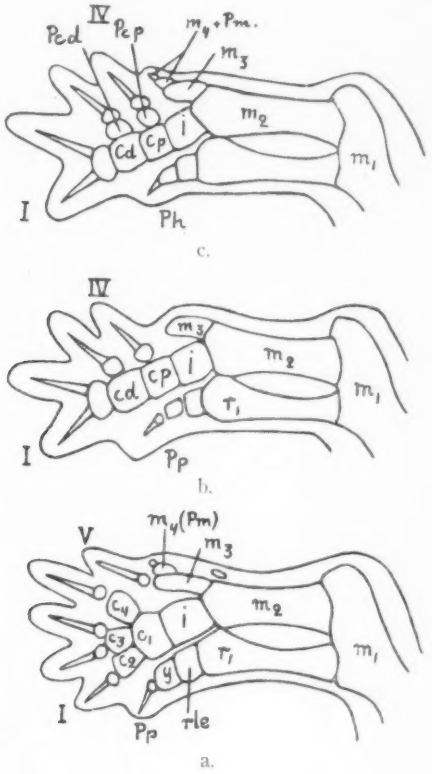

Fig. 8 a—c. Holmgren's diagrammatical representations of the tetrapod limb; a. non-urodelian limb; b. normal urodelian limb; c. urodelian limb with two "postcentrals".

process and carries two separate, identically developed pieces side by side. The two twin rays (fig. 2) are present in *Eusthenopteron* (pectoral as well as pelvic fin) and in *Sauripterus* (fig. 4) as well as in *Laugia*, and therefore may be considered as typical. In WESTOLL's deductions these two discrete elements have been thrown together into one and labelled as m_5 (fig. 7). In reality they represent—as far as we can know—two equivalent distal radials of the mesomeral axis. Transposed to the tetrapod conditions—according to WESTOLL's method—they must represent two centrals lying transversally to the unbranched series intermedium-central 1 (proximal central). The postaxial process (p_4) of m_4 was considered by WESTOLL to represent a postcentral related to m_4 (thus a *proximal* postcentral!). Thus the system of centrals, derived from the conditions in *Eusthenopteron*, must consist of a *proximal* central (c_1) and three distal centrals (c_2, c_3, c_4), forming a transverse series (fig. 8), distally to the distal end of the proximal central. And that is the condition in the embryonic limbs of all non-urodele tetrapods, where these limbs have not undergone great functional differentiations. I have demonstrated

this condition in a diagram of the anuran hand in 1933, fig. 50 b. In that paper I labelled the centrals: central 1 for the proximal central, 2, 3 and 4 for the distal row, counted from the preaxial side. In the anuran embryos the centrals 2, 3 and 4 are rather widely separated from each other and also from the central 1. This position suggests a dichotomous arrangement, especially as the system seems to be held together by mesenchymatic bands. A dichotomous arrangement is also discernible in other tetrapods, but may be more or less obscured in species of higher phylogenetical standing. It is a rule in many tetrapods (turtles, crocodiles, birds, mammals) that the centrals 2 and 3 lie close together, and often fuse, whereas the central 4 is well separated from them. That may be an expression of their different origin, as will be explained later on.

As WESTOLL has pointed out, there are many instances in my pictures of 1933, when the radiale is connected either with the intermedium or with the proximal centrale. I think that his idea of a genetical relation of the radiale with the intermedium-central axis be partly explained by this connection and that the radiale could be a result of the development of the r_3. That would explain the relations between the prepollex and the radius. But that theory lacks sufficient foundation: the connection is secondary, for instance, in some anurans (SCHMALHAUSEN) and may be so in others.[1]

This examination of the problem of the tetrapod limb along the lines proposed by WESTOLL and with the method used by him, does not give results, covering those to which he arrived.

The radials of *Neoceratodus* are undifferentiated digits see p. 500 as are the "radials" in the shark fin. From this statement follows that the most distal "radials" of the *Sauripterus* paddle are also digits. This conclusion must also be true of the two distal radials on the tip of the mesomeral axis of *Sauripterus*. If this is the case the conclusion is inevitable that the two small pieces on the tip of the mesomeral axis in *Eusthenopteron* (pectoral and pelvic fin) and in *Laugia* do not belong to the archepodium, but are digits. This conclusion is destructive to the derivation of the tetrapod limb from the *Eusthenopteron* paddle according to WESTOLL's theory, as two digits cannot form a distal central in the tetrapod limb as this theory presumes. A tetrapod limb formed with regard to this statement should only contain a proximal central and a proximal postcentral, because as has been explained earlier in this paper the intermedium (m_3 according to WESTOLL) never produces any postaxial central in tetrapods. Such a tetrapod limb is not known. The recognition of the two end radials of the mesomeral stem in *Eusthenopteron* as

[1] I therefore agree with WESTOLL's alternative fig. 7 b, according to which the radial stem develops from the tip of the radius, without connection with the intermedium-centrale stem.

digits also prohibits an explanation of the tetrapod limb as I have attempted it, strictly applying WESTOLL's method.

Another explanation is thus very desirable, and in the following I will try to build up a partly new theory.

ONTOGENETICAL STATEMENTS CONCERNING THE URODELIAN LIMBS.

Beginning with the urodeles the following embryological statements will at first be made.

1) The intermedium-centrale axis contains in primitive genera three well-defined pieces viz. intermedium, proximal and distal central.

2) The ulna of the early embryo bifurcates distally, the postaxial branch developing to the ulnare, the preaxial to the series intermedium, proximal central and distal central. This series differentiates in a cylindrical blastemic mass extending somewhat obliquely through the carpus (tarsus)[1]. The differentiation proceeds from the proximal end toward the distal, the intermedium developing first, the proximal central next and then the distal. On this intermedium-central stem no appendices of any description normally develop. The compound carpal of the first and second fingers is inserted on the end of this stem. It is already chondrified long before the chondrification of the stem has reached it.

3) The preaxial part of the carpus (tarsus) develops from the blastematic distal end of the radius and develops in a distal direction, without any contribution from neighbouring carpal (tarsal) elements. When fully developed this stem-ray consists of the radiale (tibiale) and the element y of STEINER's descriptions, to which is added an end-piece: the prepollex (prehallux) (fig. 8 b).

4) To the "stem" elements the digits (carpals, metacarpals and phalanges) are associated, of which the second develops first, then the first, followed by the third and after that the fourth and finally the fifth, if present. The two first are associated with the tip of the intermedium-central column, the third with the distal central and the fourth with the proximal central (fig. 8 b). When in the foot, the fifth digit connects with the fibulare, in all other tetrapods the sequence in the development of the digits is generally the reverse, usually beginning with the fourth.

5) In some urodeles *the feet* display irregularities in the intermedium-central complex. These irregularities seem to be rather rare and are only recorded in urodeles of more primitive phylogenetical standing. These irregularities sometimes consist in the presence of a small central on the postaxial (with regard to the intermedium-central column) side of each central, so that two pairs of

[1] This cylindric mass is suggestive of the r_2 in *Eusthenopteron* (fig. 2).

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centrals occur (fig. 8 c). The small centrals have been called by WESTOLL the proximal and the distal postcentrals respectively. Generally one or other of these postaxial centrals is absent, in most cases the proximal. The feet generally have five toes. A postminimus also occurs, and sometimes a post-postminimus. In the hand postcentrals seem never to have been recorded. Normally the hand has always four fingers only. A fifth finger has only once been found in an abnormal urodelian hand (ZWICK, 1898). A pisiforme never occurs in the hand.

6) The abnormal "postcentrals" in the feet of the embryos of *Megalobatrachus* are certainly due to a peculiar mode of growth in width of the central complex (HOLMGREN, 1936). Such is probably the case as well in *Hynobius* (*Salamandrella*). In the latter the centrals when growing in width are "open" on the postaxial side, that is, they have no perichondrium on that side. Occasionally then the "outflowing" prochondrial tissue becomes cut off from the rest of its centre and becomes a "postcentral". In *Megalobatrachus*, where there is generally one or two axial centrals in the adult foot, the process of lateral growth of these centrals begins with protuberant parts of the rudiment. These protuberant portions generally fuse again with the real centrals causing them to augment their width. Occasionally, however, such protuberant portions are cut off from the real central proper, forming "postcentrals". Even if these "postcentrals" serve the purpose of broadening the tarsus, it is not a priori excluded that they may have a phylogenetical value besides.

7) In *Hynobius* and other primitive Salamanders the limbs of young larvae are rather broad and fin-like, very reminiscent of a *Neoceratodus*-fin, but in reversed position (fig. 9).

THE STEGOCEPHALIAN LIMB, IN THE LIGHT OF WESTOLL'S THEORY STRICTLY APPLIED.

When attempting a comparison between the rhipidistid paddle and the urodele limb, we immediately meet with a great difficulty. The paddle has four mesomeral segments, the urodele limb five, if we assume that the intermedium-central column belongs to the mesomeral axis. WESTOLL has got round this difference by assuming a fusion of the two twin end rays of the mesomeral stem, to form a fifth mesomere or assuming one of the two rays to be a mesomere. In this way a fifth mesomere will undoubtedly arise, but we have simultaneously departed from reality. But if we assume the possibility of a fusion, another difficulty arises. In the *Eusthenopteron* paddle postaxial processes are only present on the mesomeres 3 and 4. The mesomere 3 answers to the intermedium, which never has postaxial outgrowths in tetrapods. The mesomere 4, that is the proximal central, must then carry the only postcentral

of the tetrapod limb resulting from the rhipidistian paddle. This postcentral must be a *proximal* postcentral. A distal postcentral could never arise, as we are not scientifically justified in assuming that the two supposed fused end rays should have produced a postaxial outgrowth, which would have to substantiate a distal postcentral. Thus in this way we do not arrive at an urodelian limb, *but we arrive at a stegocephalian* such as that of *Eryops,* where the centrals 2 and 3 are supposed to be fused to form the fifth mesomere, and the *proximal* postcentral the small postaxial central. And this type is that of all non-urodelian tetrapods. The possiblity of the fusion of the centrals 2 and 3 is demonstrated by the mammals, where the centrals 2 and 3 generally become fused secondarily, during the development or are already fused when first appearing in the early embryo. As the *Eryops* hand has many times been compared with those rare cases of *Megalobatrachus,* with three centrals, it must here be strongly emphasized that in the *Megalobatrachus* case the centrals are the proximal and distal axial centrals and the *distal* postcentral, whereas *Eryops* has the *proximal* postcentral (central 4). My earlier assumption that the postcentral of *Eryops* was fused with the fourth carpal is not necessary, if we proceed according to WESTOLL's lines. But those lines do not lead to a satisfactory explanation, as will be tolerably clear in the following pages.

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THE URODELE LIMB.

Now, turning our attention to the urodelians, we will at first stress the following points.

1) The axis contains five elements.

2) The central axis develops successively a cylindrical blastema, extending from the ulna, through the intermedium, the proximal and the distal centrals to the rudiment of the carpal 1 + 2.

3) The centrale prepollicis develops through segmentation from the primordium of the radiale, which develops from the distal end of the radius.

From these statements the conclusion must be drawn that the primitive urodele limb must have been composed of at least five axial pieces generally without processes. The second of these pieces must have carried a preaxial and a postaxial portion. Digits join the axis, preaxially (first digit) as well as postaxially (second to fourth or fifth digits).

A fish fin of this description is not known. That of the crossopterygians is to short (one mesomere missing) and that of *Neoceratodus* too long. Nevertheless the *Neoceratodus*-fin is better adapted to serve for comparison with the urodele limb than the crossopterygian paddle, *as it is provided with rays* arranged along the axis, preaxially as well as postaxially, whereas in the rhipidistids the radials, as in *Sauripterus,* are placed only preaxially as referred

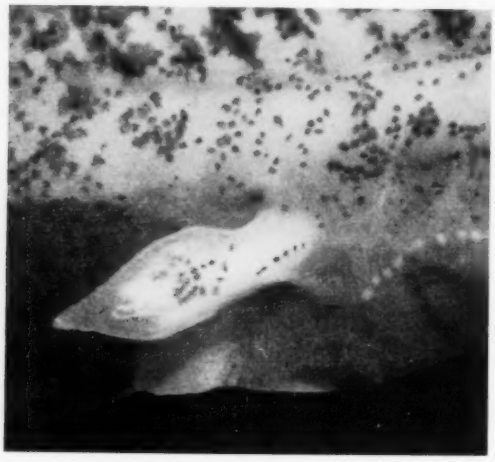

Fig. 9. Pelvic "paddle" of the larval *Hynobius retardatus*.

to in the mesomeral axis. In *Neoceratodus* the rays develop from blastemas well separated from the axis (HOLMGREN, 1933). During their development they come nearer to the axis ultimately to become articulated against it. *These rays thus develop principally as the urodele digits.* In an adult *Neoceratodus* fin the rays are normally placed one on each side of the distal end of every joint (excepting the most distal ones) along the axis. I have demonstrated (1933) how to explain the urodele limb in the light of that of *Neoceratodus*. According to that explanation the normal urodelian limb may have arisen from a short "archipterygium" containing at least five joints[1], with two digits on the tip and in addition one postaxial digit on each of joints four and five. In this "archipterygium" a radial stem and an ulnare outgrowth were present, exactly as in *Neoceratodus:* The occurence of a long pointed end portion of the larval limb in *Hynobius* (*Salamandrella*) explains my assumption that the ancestral "archipterygium" contained more than five joints, of which, however, those beyond the fifth disappeared. This assumption has now got a certain confirmation through the following observations on the blood-plexus of a typical larval foot of *Hynobius retardatus* (30 mm long) (fig. 9). The fig. 10 is a reduced graphical reconstruction of this foot, made from a 5 μ series of sections at 80 $\times$ magnification.

The tarsus is entered by six main blood vessels viz. one fibular (*fB*) and one tibial (*tB*) border vessel, three medial vessels (E_{1-3}) on the extensor side between the tibia and fibula and one (*Fl*) on the flexorside also between tibia and fibula. The border vessels run distally to the level of the rudiment of the

[1] As there are only three myomeres giving attribution to the *Neoceratodus* pectoral fin, it is highly probable, that its long axis is a secondary modification (cf. WESTOLL).

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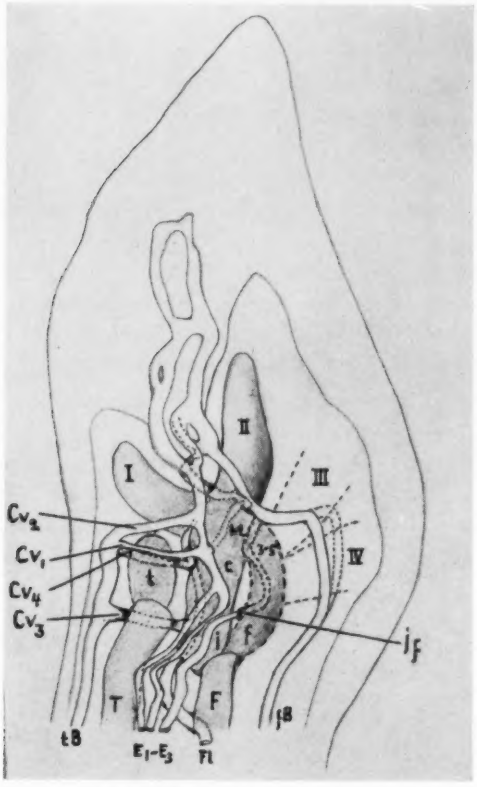

Fig. 10. Blood vessels in the "paddle" of the larva of *Hynobius*.

joined tarsals of the first and second toe. Here they both turn mediad to join the system of the medial vessels. The tibial border vessel has two connections (cv_1, cv_2) with the medial vessels on the extensor side and two (cv_3, cv_4) with the vessel on the flexor side of the foot. The fibular border vessel has only one connection with the medial system, viz. at the proximal end of the fibular side of the second toe rudiment. The two (medial) tibial vessels of the extensor side (E_1, E_2) join over the centrale column of the tarsus and the common vessel runs distad collecting the two vessels (Cv_1, Cv_2) from the tibial border vessel, then continuing apicalward in an apical direction. The third medial vessel (E_3) on the extensor side also runs frontad, in the beginning together with the two others, but turning to the flexor side reaching it in the angle between the future fibulare and intermedium through a space; the future intertarsal-foramen (If). Then the vessel continues distad near the epithelium of the flexor side, thus on the lower side of the blastema of the future tarsalia 3—5. After passing these the vessel turns upward and joins the fibular border vessel

at the basis of the second toe. From this same point two branches turn downward toward the flexor side. One of them crosses the flexor side of the rudiment of the carpals 1 + 2 and then joins the common medial vessel of the extensor side at the proximal border of the carpal 1+2. The other runs below the distal end of the second finger. The main vessel (*F1*) of the flexor side runs frontad, communicating twice (*Cv*$_3$, *Cv*$_5$) with the tibial border vessel and then turns upward joining the main medial vessel of the extensor side. Thus when reaching the angle between the first and the second finger rudiments, the blood system chiefly consists of two blood vessels, one on the tibial and one on the fibular side of the intermedium-centrale column. These two vessels now continue distad side by side joined with each other through commissures which bend toward the flexor side. *The two vessels continue distad past the tip of the second toe and with a general direction toward the tip of the foot.* As this projecting part of the vascular systems obliterates long before the tip of the limb has attained its full length, these projecting vessels can scarcely have any essential importance for the growth of the tip of the limb. I, therefore, interpret these vessels as rudimentary remains of a system which once accompanied a reduced tip portion of the intermedium-centrale stem in the same way as the proximal part of the same system does concerning the persisting parts of the same stem.

THE ORIENTATION OF THE PECTORAL FIN IN LIVING DIPNOANS.

Before summing up the results of the previous investigation, I want to say some words about the orientation of the dipnoan pectoral fins. In *Neoceratodus* the pectoral fin is—as is well known—inserted so that, in a trailing position, it has its axis ventrally and its preaxial border dorsally[1], thus contrary to the position of the paddle in the crossopterygians and the larval anterior limb in the urodeles. In the pelvic fin the orientation is the same as in the crossopterygians. If a *Neoceratodus* fin, thus, should transform into a tetrapod limb it must be twisted twice, whereas the urodelian limb rudiment only needs to be twisted once.

This puzzling fact, however, loses some of its importance, when stating that the pectoral fin of *Protopterus* has another orientation, with the strong axis, in a trailing position, forming the external and the soft preaxial border, the internal border of the fin. The fin is thus carried practically horizontally. The movements of the *Protopterus* fin are very varying. The fin can take any

[1] In 12—15 mm embryos the preaxial border is turned dorsolaterad and its postaxial ventro-mediad. In earlier stages the fin rudiment is horizontal. During the following development the posterior part of the rudiment is carried ventrad instead of dorsad (as is the case with the pelvic fin in *Neoceratodus*).

position from the horizontal fronto-caudal to the horizontal caudo-frontal direction. This great mobility of the fin depends on its great ability for basal rotations. Normally the humerus is directed more or less perpendicular to the body wall, with ability for movements especially in a frontal or caudal, but also in a dorsal and ventral, direction. The joint between the humerus and the second piece of the axis consists of a concavity on the humerus, into which the spherical proximal end of the second joint fits. This articulation allows considerable rotation. When extended frontad the preaxial border is generally held ventrad, but may also be directed mediad. When using the fin as an oar, the preaxial border is mostly turned dorsad, but may also be turned ventrad. These observations, made on living animals, seem to indicate that the position of the *Protopterus* fin is something intermediate between that of *Neoceratodus* and that of the crossopterygians. WESTOLL has suggested as well that the position of the *Scaumenacia*-pectoral was that of a crossopterygian. Thus the position of the *Neoceratodus* pectoral fin does not form an obstacle towards deriving the urodele limb from the dipnoan fin.

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THE PRE-TETRAPOD POSTERIOR LIMB WAS STRONGER THAN THE ANTERIOR.

Another point of view that may in some way affect our interpretation of the phylogeny of the tetrapod limb is the following. In all crossopterygians the pectoral fins are stronger than the pelvic. In *Eusthenopteron* the skeleton of the pelvic fin is apparently reduced as compared with that in the pectoral. In the lower tetrapods the contrary is the rule. In the dipnoans the pelvic fin is generally shorter than the pectoral, but in *Scaumenacia* the contrary seems to occur. From this point of view a derivation of tetrapods from dipnoans does not seem to be excluded. But as long as the endoskeleton is unknown, no conclusion may be drawn from such facts. All tetrapods, however, were probably derived from fishes with the pelvic fins stronger than or at least as strong as the pectoral ones.

COMPARISON OF THE LIMB OF URODELES AND OTHER TETRAPODS.

Urodeles.	*Anurans and amniotes.*
1) The digits develop in *postaxial* direction (referred to the intermedium-centrale axis) from the second to the fourth or fifth.	1) The digits develop from the fourth (or third) in *preaxial* direction to the first.

2) Hand and foot homodynamously developed.

3) The hand has never more than four fingers. A pisiform never occurs.

4) The foot has always five toes, or four and a remainder of the fifth. A postminimus always occurs and sometimes a post-postminimus. The tarsus is arranged as the carpus.

5) The intermedium-centrale complex forms a two- or three-segmented, unbranched column. When accessory centrals are present, they form a series parallel with the axis.

6) The intermedium-central complex develops from a rodlike blastema and its parts develop successively in an apical direction.

2) Hand and foot (very) differently developed (except in Stegocephalians).

3) In recent species the hand has generally five fingers, or at least four with rudiments of the fifth (Anurans). A pisiforme is generally present.

4) The foot has generally five toes. A postminimus may be present. The tarsus is fully arranged as the carpus in the Stegocephalians only.

5) The intermedium-centrale complex consists of two axial (an intermedium and a proximal central (c_1) and three distal pieces (c_2, c_3, c_4), the latter located more or less perpendiculary to the former.

6) The components of the intermedium-central complex generally develop separately, in different blastemas.

ARCHEPODIUM AND NEOPODIUM IN THE CROSSOPTERYGIANS.

One of the most important problems regarding the rhipidistid paddle is to decide, what is the stem (archepodium) and what the rays or digits (neopodium). WESTOLL has answered this question for *Eusthenopteron*, trying to demonstrate that about all the skeletal parts of its paddle are used up, forming the stem in the tetrapod limb. The present writer came to practically the same result, working along the lines of WESTOLL. But now arises the very important question: what are stem and rays in *Sauripterus?* A comparison with *Eusthenopteron* shows that the paddle of these two is formed according to the same pattern and that nearly all the structures of the *Eusthenopteron* paddle are present in *Sauripterus*, but in the latter there are numerous pieces which are not present in *Eusthenopteron*. Do these also belong to the archepodium? If they do not, as must be the consequence of WESTOLL's theory, they must be rays (radials) of some sort. In *Neoceratodus* (and also in *Spinax*) I have (1933) shown *that the "radials" develop as true digits from separate primordia* which attach secondarily at the stem. If that was also the case in *Sauripterus*,

the problem of the tetrapod limb acquires a new aspect. Then in that case the rays in *Sauripterus* are almost all *preaxial* and the consequence is that they must have been that too in the predecessors of *Eusthenopteron*. There must at least have been a preaxially-located tissue with digit-forming potentiality in these predecessors. According to WESTOLL's theory the mesomeral axis in the pre-tetrapod stage should turn inward. At that time it would be possible that the paddle moved over to the preaxial side independent of this tissue which in that way should shift to the postaxial side of the mesomeral stem and there produce postaxial rays, or a quite new digit-tissue should develop on the postaxial side. If we accept the former of these possibilities, we come from Scylla to Charybdis, then in that case the series of digits must be reversed so that the fourth or fifth preaxial digit became the first and the first the fourth or fifth. This way thus leads to a sharp distinction between the urodelian and the non-urodelian limbs, the former with primary postaxial, the latter with primary preaxial digits. And that conclusion cannot be accepted according to WESTOLL's theory. It is very improbable that the digits of the pre-tetrapod limb should be quite new formations, without predecessors in the fishes. But nevertheless accepting this, it must be born in mind that this cannot have validity for the urodeles, the limb structure of which is easily explained from the conditions in dipnoans, without assuming any new formation of radials (digits).

If we, nevertheless, accept the standpoint that the tetrapod digits are new formations, it is hard to believe that these digits when appearing should avoid the preexisting radials and select to insert upon the side of the paddle, where there were (almost) no radials at all.

In the Selachians (and also partly in *Neoceratodus*) the preaxial rays develop from basally towards the apex, whereas the postaxial rays develop in the opposite direction. Applying this statement to the tetrapod limb, the digits should be postaxial in the urodeles as they develop from the tip basally, preaxial in the other tetrapods where they develop in reversed direction. And that cannot be accepted from WESTOLL's standpoint. But it is fully in accord with my theories of 1933, according to which the sequence of the digits is quite different in urodeles and non-urodeles. My theory, however, accepted a branched intermedium-centrale complex with no real apex and not developed from the postaxial mesomeral axis. The latter I consider reduced in its distal portions (ulnare, pisiforme, fibulare-postminimus, answering to the mesomeres 3 and 4 in *Eusthenopteron*).

EARLY ONTOGENETICAL STAGES OF THE URODELE LIMB, COMPARED WITH THE RHIPIDISTID PADDLE.

In the urodele embryo the ulna divides apically into two branches: a postaxial, giving rise to the ulnare, and a preaxial from which the intermedium-central column develops. In *Neoceratodus* the ulna also has two branches, a small postaxial, answering to the ulnare, and a preaxial which is the long general axis of the fin. A comparison with the urodeles then led me to consider the long axis as being the intermedium-centrale axis. In the crossopterygians the ulna of the adult has two special branches: one postaxial and one preaxial. The postaxial consists of two joints, of which the apical carries two "radials". The preaxial, unbranched in *Eusthenopteron*, carries two "radials" in *Sauripterus*. In anurans and in the posterior limb of urodeles the pisiforme or postminimus develops in connection with the ulnare resp. fibulare and may be described as a joint belonging to the ulnare axis, but developing in a palmar direction. When a fifth digit developed, it became connected with the ulnare, lying level with it and not with the pisiforme. Thus in the anurans the ulnare stem contains two skeleton pieces with which a digit may be articulated. In the anurans I found the intermedium-centrale complex dichotomously arranged, as is the general arrangement in *Sauripterus*. To the question of the ulnare axis may be added that I figured (1933, fig. 9) a *Neoceratodus* pectoral fin (fig. 6), where a skeletal piece with two digits articulated with the ulnare portion of the second joint. This piece ($?m_4$), of course, may be composed by the basal joints of the two digits but that may not be of great consequence as we do not know the original status of the m_4 in the crossopterygians.

THE "INTURNING" OF THE MESOMERAL AXIS.

WESTOLL says that "the entire basis of HOLMGREN's argument is removed by the recognition of the inturning of the mesomeral axis during the evolution of the rhipidistid paddle into a tetrapod limb, and the urodeles actually retain, better than most other tetrapods, primitive characters shown also in the stegocephalian limb".

The alleged inturning of the mesomeral axis should be of great interest and strong evidence for the theories of GREGORY and WESTOLL, if there was any ontogenetical evidence for it. But there is none, as the intermedium-centrale axis always develops at the preaxial corner of the ulna, inturned from its very first appearance. This "inturning" is the entire basis of WESTOLL's theory regarding the nature of the intermedium-centrale complex. The "inturning" hypothesis disregards the fact that there is another axis present at the post-

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axial border of the tetrapod limb viz. the axis ulnare-pisiforme (fibulare-postminimus). This axis must represent the border-axis or mesomeral axis of the tetrapod limb. It is reduced and especially regarding the pisiforme bent in a palmar direction and has no superficial likeness with the mesomeral axis of *Eusthenopteron*, but, nevertheless, must correspond to it theoretically.

POSTMINIMUS AND PISIFORME.

In spite of the pliability with which WESTOLL's theory makes the crossopterygian paddle fit in the tetrapod pattern, I am not able to accept it, though, with my strict application of it, the result would be the very best confirmation of my theory of the double origin of the tetrapod limb, the one from a dipnoan, the other from a crossopterygian paddle. The account that WESTOLL has given of the pisiforme and postminimus results in the thesis: "It seems safest to regard the post-postminimus and pisiform as secondary developments, at least in their usual position and relations." The reasons upon which this conclusion is based are not very strong. "The nature of the 'postminimals' is less clear. In the feet of certain tetrapods (e.g. many urodeles, fig. 4 E, F), there is a postminimal (sensu stricto) lying immediately lateral to the fifth tarsal, which can be plausibly regarded as a 'sixth' tarsal; there may also be a post-postminimus which is closely related to the disto-lateral corner of the fibula. The latter may well be of no phylogenetical significance, a possible sesamoid. In the hand only one element is identified—the pisiform. In the ontogeny of some tetrapods (cf. HOLMGREN, 1933, for figs.) the pisiform appears to develop laterally to the ulnare, so that it is almost in line with the postaxial carpalia (e.g. in *Telmatobius*) whereas in most forms the pisiform is essentially wedged between the ulna and ulnare. It may therefore correspond in position either to the postminimus or to the post-postminimus of the foot, and may be a secondary (sesamoid) development. There is also the possibility that it represents a true serial homologue of the carpal series in primitive forms (cf. perhaps a postminimus) which has become displaced and specialised in relation to muscular actions." "The nature of the various postminimal elements is much more ... doubtful, and only the true postminimals of the foot are really comparable with the tarsalia." In this summary there is not much on which to build up a theory about the pisiforme and the postminimals. On every line one meets uncertainties or misinterpretations. I, however, regarded them as homodynamously developed typical elements of the tetrapod limb. For the present paper I have reexamined my series of embryological material and made some statements. 1. There cannot be a question of any sesamoid elements in the carpus and tarsus of the amphibians, as the alleged "sesamoids" develop contemporaneously with the other elements of the carpus and tarsus in these ani-

mals where otherwise no "sesamoids' occur. Their regular existence in the urodelian feet and in the hand (and foot) of the anurans, reptiles, (birds) and mammals must signify that they are "normal" elements, belonging to the tetrapod pattern.[1] 2. The postminimus of the urodelian foot is no "sixth" tarsal, though it seems to lie immediately lateral to the fifth tarsal. In reality it lies at the distal end of the ulnare from which it develops in a latero-plantar direction. In *Hynobius* it may carry a short endpiece (HOLMGREN, 1936). It cannot be considered as a sixth tarsal because of its relation to the muscles of the tarsus. The *musculus extensor cruris et tarsi fibularis,* which inserts on the border of the fibula, extends distad to the fibulare, inserting on it, then having reached the postminimus inserting on it with a segmented-off portion. This muscle is the fibular border muscle or stem muscle which effectuates the outward turning of the foot. *The m. extensor digitorum communis* which works the extension of the toes and partly inserts on the tarsals, passes the postminimus without insertion. The behavior of the *m. extensor cruris et tarsi fibularis* gives strong evidence for the postminimus as a stem portion of the tarsus. On the tibial side of the tarsus the *m. extensor cruris tibialis,* inserting on the prehallux, effects the movement of the foot in preaxial direction and thus is antagonistic to the *m. tarsi fibularis.*

And now to the pisiforme. The urodeles never have a pisiforme. But in all other classes of tetrapods a pisiforme seems to be a regular carpal element. It never develops in line with the postaxial carpalia, but lies below the level of these bones. In anurans it always develops in connection with the ulnare, usually on its lower side, where it is mostly connected with it. Ontogenetically it buds out from the ulnare, at about a right angle from its distal end, but in *Telmatobius* it is situated distolateral to the ulnare but much deeper than the fifth carpal, and there can be no question of its belonging to the carpal series. In *Pelobates* the pisiforme lies just below the ulnare, in *Rana* and *Bufo* it is turned somewhat inward. The morphological significance of the pisiforme becomes rather clear when we state that it is in anurans the place of insertion for the volar part of the *Musculus extensor carpi ulnaris,* the carpal representative of the tarsal *m. extensor cruris et tarsi fibularis.*

A comparison between the pisiforme and the postminimus must give the result that they are homologous structures and, thus, that the pisiforme belongs to the very reduced mesomeral axis of the hand. In some mammals the pisiforme is provided with an end joint, e.g. in *Pedetes caffer,* where this end joint in addition carries a broad palmar nail. The postminimus was found in *Mus* to fuse with the fibulare and centrale 4 forming together with these the calcaneus, on which a postminimal end-piece sometimes may be present (certain rodents).

[1] The characterization of a skeletal element as "sesamoid" gives no explanation but is many times apt to obscure morphological conditions.

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The post-postminimus is a rare occurence and seems only to have been recorded from *Cryptobranchus*. It is located upon the postaxial corner of the distal end of the fibula, at the place where the ulnare rudiment should develop according to WESTOLL's theory. It seems excluded that the post-postminimus should be a sesamoid.

The result of this discussion is that the ulnare-pisiforme and the fibulare-postminimus represent the m_3 and m_4 of the mesomeral axis of the crossopterygian paddle.

MY IMPROVED THEORY OF THE PRIMITIVE TETRAPOD LIMB.

The preceding discussion gives no other contributions regarding the derivation of the urodele limb from a dipnoan-like paddle of the *Neoceratodus* type than that this dipnoan paddle must have had a much shorter intermedium-centrale axis than *Neoceratodus* and that its mesomeral axis must have been very strongly reduced. The intermedium-centrale axis answers to the radial r_2 of *Eusthenopteron*, which is supposed by GREGORY and RAVEN and WESTOLL to disappear.

The question of the development of the limb of all other tetrapods is much more complicated as seen from the preceding pages. So much, however, seems to be clear that the theories of GREGORY and RAVEN and WESTOLL cannot be accepted as they are too constructive. The recognition that the mesomeral axis in the tetrapods consists of the humerus (femur) (m_1), the ulna (fibula) (m_2), the ulnare (fibulare) (m_3), the pisiforme or postminimus (m_4) and in some cases an end joint on the postminimus (m_5?), gives quite a new aspect to the problem. Assuming a mesomeral axis of this description, the hypothesis of the "inturning" of the mesomeral axis in the tetrapod limb falls away. This hypothesis is already highly doubtful as there is nothing in the ontogeney that supports it. On the contrary, the ontogeny seems to contradict it. Now, advancing the problem from my standpoint and using the *Sauripterus* paddle as a starting point, we shall find that this paddle contains all the requisita of a tetrapod limb of the non-urodelian type. The only things which need to be altered are the number of *distal* rays (digits) and the dividing of the r_2 in two pieces (intermedium and centrale 1). It is not necessary to assume that the digits are neomorphs or to put on the digits where they are convenient to the theory. Neither need it be assumed that the ulnare has developed from a non-existing postaxial process on the m_3, nor is it necessary to transform the post-axial muscular processes (or supports for horny rays) of the m_3 and m_4 into centrals. Nor must the r_2 and r_3 be allowed to disappear or be transformed into prepollex portions. Neither is it necessary to let the end radials of the mesomeral stem fuse to form a distal central (m_5).

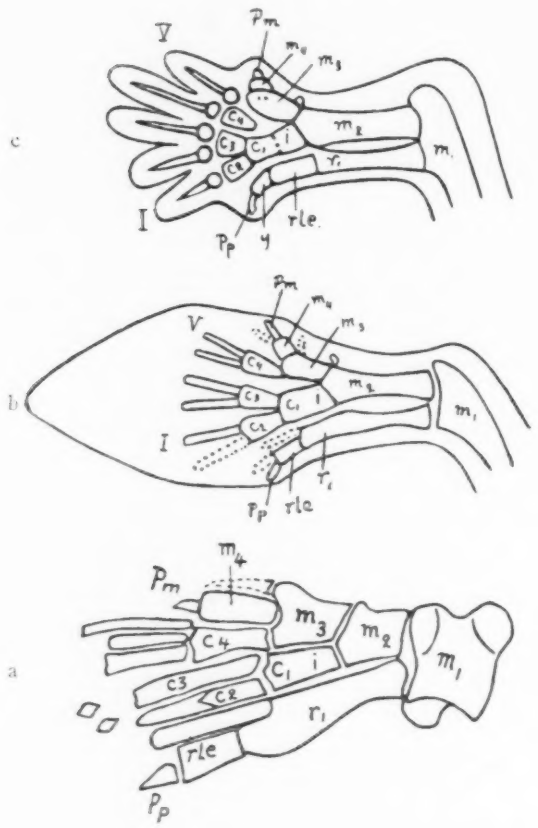

Fig. 11 a—c. Holmgren's new interpretation of the development of the tetrapod limb from a crossopterygian paddle like that of *Sauripterus*. a. the *Sauripterus* paddle; b. the same with shortened mesomeral axis; reducing rays with broken outlines; c. the tetrapod limb. Mesomeral axis ending with the postminimus or pisiforme.

The fig. 11 b demonstrates a *Sauripterus* fin imagined with a reduced mesomeral axis. In this fin the intermedium centrale complex has become dominant as it is in the non-urodelian tetrapod limb. The r_2 of the *Eusthenopteron* paddle (fig. 2) is represented by one preaxial branch ($i+c_1$) on the distal end of the ulna, this branch carrying two centrals (centrals 2 and 3) which support four distal radials. On the preaxial side of the distal end of the ulnare (m_3) the r_3 represents a third distal central (central 4), this too having two distal radials. The centrals 2—4 of my original theory were all thought to be carried by the intermedium-centrale stem and to be parts of a dichotomously-branched tree, as they really seem to be in early ontogenetical tetrapod stages. In preceding pages I have, however, pointed out that the central 4 seems to

have a certain distinction with regard to the others, as it develops separated from them. Reviewing my old sections I have now found that there is a certain relation between the ulnare or fibulare with the fourth central. In some cases these pieces are very closely related to one another. In *Pelobates* the ulna and the central 4 in certain sections can scarcely be separated, the same is true concerning *Rana* and *Xenopus* (also in the foot), *Chrysemys, Agama,* birds and many mammals (in the hand as well as in the foot). These observations induce me at present to consider the central 4 as being originally a dependent (r_3) of the otherwise reduced mesomeral axis. As the mesomeral axis got reduced (fig. 11 b) its r_3 became independent and associated with the intermedium-centrale stem and became the central 4 of this stem (fig. 11 c), generally carrying the digits 4 and 5. As the r_3 shifted in a preaxial direction, the external of its radials could gain attachment on the ulnare, as for instance in the Chelonians. The improved theory presupposes the following losses of the *Sauripterus* paddle: an unnamed piece on the postaxial distal corner of the m_3, one of the end radials on m_4, one of the radials on the second central (piece bb in GREGORY's and RAVEN's nomenclature), one radial on the postaxial side of the r_1, and one end radial on the r_2 system. As the radials are the most variable parts of a fin, the disappearance of some of them is of very little consequence. My theory also assumes the dividing of the intermedium-centrale stem in two pieces: intermedium and centrale 1 (fig. 11 c).

According to my theory all the distal radials[1] in the *Sauripterus* paddle are true digits, as are the radials in sharks and *Neoceratodus*. They are all (excepting that of the postminimus) preaxial radials with regard to the mesomeral stem. Also in the urodele limb all digits are preaxially located in relation to the very reduced mesomeral axis, postaxial (excepting the first) with regard to the intermedium-centrale axis.

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[1] Perhaps with exception of the postaxial piece on the distal end of m_3 in *Sauripterus*.

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ABBREVIATIONS.

c central column
c_1 proximal central
c_2, c_3, c_4 distal centrals
cd distal central
cp proximal central
cv_1—cv_4 communicating blood-vessels
E_{1-2} vessel on the extensor side
F fibula
f fibulare
fB fibular border vessel
Fl vessel on the flexor side
H humerus
I intermedium (r_2)
If intertarsal foramen
m_1, m_2, m_3, m_4 mesomeres 1—4
p_2, p_3, p_4 postaxial rays of metameres
pcd, *Pcd* distal postcentral
pcp, *Pcp* proximal postcentrals
Ph prehallux
Pm postminimus
Pp prepollex
ppm post-postminimus
prc precentral
R radius
r_1, r_2, r_3 preaxial rays of mesomeres
rle radiale
T tibia
t tibiale
t.B. tibial border vessel
U ulna
u ulnare
y centrale prepollicis (y)
I, *II*, *III*, *IV*, *V* diggits I—V
1 + 2 tarsale 1 + 2
3, *4*, *5* tarsalia 3—5

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